USING *ACACIA* AS A NURSE CROP FOR RE-ESTABLISHING NATIVE-TREE SPECIES PLANTATION ON DEGRADED LANDS IN VIETNAM

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ABSTRACT

Acacia mangium, *A. auriculiformis* and their hybrid, the leguminous fast-growing tree species has been widely adopted as a nurse crop for re-establishing native-tree plantations on degraded lands in Vietnam, but with little success. This may be attributed to not fully understanding the site requirements of target native species and the potential for negative as well as positive between-species interactions. The most planted native species is *Hopea odorata* Roxb., a dipterocarp that is thought to be shade-tolerant. To resolve how best to apply and manage such a system of mixed-species silviculture, this study first investigated the resource requirements of *H. odorata* in its natural habitat and how degraded soils change under consecutive short-rotations of *A.* hybrid plantations. Plantings of *H. odorata* within circular and strip gaps in 3- and 2.5-yr-old *A.* hybrid plantations, respectively, were used to assess the growth and physiological responses of *H. odorata* to competition for light and water. The light gradients created in the circular-gap experiment and the different light condition in the strip-gap experiment were used to assess how changes in growth rate were associated with the efficiency of use of light by the *H.odorata*.

Site requirements for regeneration of *H. odorata* were investigated in its natural habitat in three representative 50 × 50 m inventory plots in a secondary evergreen natural forest in southern Vietnam. The upper canopy was dominated by four dipterocarp species; *H. odorata*, *Shorea roxburghii* G. Don., *Anisoptera costata* Korth., and *Dipterocarpus alatus* Roxb. ex G. Don. The prevailing stand structure supported the vigorous germination, but not development of *H. odorata* seedlings due to low levels of light near the forest floor. Seedling germination was supported when daily transmitted photosynthetically active radiation (PAR) was between 2.2% and 6.6%, but seedling

development was only observed when PAR was 11.4%. The slightly acidic sandy soils with low nutrient concentration were apparently not a constraint on growth of *H. odorata* seedlings given adequate light conditions. The results suggest that the re-establishment of *H. odorata* on degraded sites using nurse crops should be possible provided that high levels of shading are avoided.

The potential to improve soil conditions with *Acacia* hybrid was assessed on degraded gravelly and sandy soils in Central Vietnam, from second- or third-rotation plantations representative of five age classes (0.5- to 5-yr old) and adjacent abandoned lands as controls. Compared to abandoned land, stock of total soil carbon, total nitrogen, and exchangeable calcium, magnesium and sodium were significantly higher in some years of the 5-yr rotation. However, extractable phosphorus and exchangeable potassium were not affected. Electrical conductivity was significantly higher and bulk density was significantly lower in all ages. Soil pH_{CaCl2} was lower at ages 0.5 and 5 yrs, and pH_{H2O} at age 5 yrs. Within a rotation, most soil properties did not change significantly with plantation age, although they appeared to decrease during the first three years; total carbon then recovered to initial levels, but total nitrogen and exchangeable cations remained lower. Some soil properties were strongly related to gravel content and elevation, but not with growth rate. Thus consecutive plantings of short-rotation *Acacia* hybrid on degraded and abandoned land can lead to changes in some soil properties.

Growth and physiological responses of *H. odorata* to different environmental conditions created in a nurse-crop plantation were examined in a field experiment where *H. odorata* seedlings were planted within three 22 m-diameter gaps opened in a 3-yr-old *Acacia* hybrid plantation in Central Vietnam. At age 2 yrs, stem diameter, total height

and crown diameter of the *H. odorata* increased significantly from gap perimeter (GP) to gap centre (GC). This positive response correlated with significant increases in daily incident photosynthetically active radiation (PAR) from 24% to 61% of total incident PAR. Net photosynthetic rate at 1500 μmol m^{-2} s^{-1} (A_{1500}) and stomatal conductance (g_s) were significantly lower for trees near the GP than those near the GC. Light-saturated photosynthesis (A_{sat}) was significantly lower for trees near the GP than GC at age 1 yr, but not at age 2 yrs. Apparent quantum yield (Φ), dark respiration (R_{dark}), and photosynthetic biochemical parameters (V_{cmax} and J_{max}) were similar between treatments. Chlorophyll content, chlorophyll fluorescence (F_v/F_m), and leaf N and P concentrations were also unaffected by treatment. Nevertheless, specific leaf area was higher in the GP than other treatments. Despite the substantial difference in PAR between treatments, trees near the GP received levels of irradiation >500 μmol m^{-2} s^{-1} for 12% of the day *v.* 38% at the GC. Significant reductions of leaf water potential (Ψ_{leaf}) at the end of the dry season in treatments close to the GP compared to those near the GC suggested competition for water between *H. odorata* and the acacia nurse trees, although pre-dawn Ψ_{leaf} remained >-0.5 MPa. Thus, despite being a species that regenerates naturally in shade, *H. odorata* quickly acclimates to much higher light environments.

Understanding how *H. odorata* alters its architectural traits and growth rate in response to changing light environments is essential when designing and manipulating mixed-species plantations containing this species. Seedlings of *H. odorata* were planted into the circular gaps referred to above, and in 5 and 7.5 m strip gaps within a 2.5-yr-old *A.* hybrid plantation. Crown structure, absorption of photosynthetically active radiation (APAR) and whole-plant light-use efficiency (LUE; above-ground biomass growth or wood growth per unit APAR) of the seedlings over a gradient of light across the circular gap were examined for two years. Biomass production increased exponentially from the

GP to the GC. This was largely due to an exponential increase in APAR and a minor increase in LUE. The large increase in APAR was associated with an increase in leaf area and a reduction in shading from the nurse trees. Conversely, APAR per unit leaf area decreased towards the gap centre, probably due to steeper branch and leaf angles in order to avoid high radiation. In the strip-gap planting, the PAR was similar to that at the perimeter of the circular gaps; however the light pattern was dominated by sun flecks in the strip gap and direct sunlight in the circular gap. While the LUE of the more shaded *H. odorata* trees in the strip gaps was much higher, this was not enough to make up for the much lower APAR and hence biomass production. This study shows that *H. odorata* is able to grow under a wide range of PAR and that the availability of PAR has a strong influence on its growth. While the strip gaps used in this study appeared to be too narrow, the circular gap indicated that nurse plantings are an effective silvicultural design for establishing *H. odorata* provided that competition for other resources is managed.

The study concluded that *Acacia* hybrid is a potential species for recovery of some key soil chemical and physical properties. It is a potential nurse crop for re-establishment of native-tree species on degraded lands. Although *H. odorata* is shade-adapted species, it has great plasticity to acclimate to a range of light environments. However for mixed-species systems using these species, interspecific competition for light and soil water between *A.* hybrid and *H. odorata* needs to be addressed during the design and then management of the plantations.

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ABBREVIATIONS

ACIAR	Australian Centre for International Agricultural Research
AGB	above ground biomass
A_{max}	maximum photosynthetic rate
APAR	absorption of photosynthetically active radiation
A_{sat}	light-saturated photosynthesis
BA_b	branch basal area
BD	bulk density
C:N	carbon:nitrogen ratio
C_a	ambient CO_2 partial pressure
chl	chlorophyll
C_i	intercellular CO_2 partial pressure
$D_{0.3}$	diameter at 0.3 m above ground
DBH; $D_{1.3}$	diameter at breast height
D_c	crown diameter
EC	electrical conductivity
Ex-Ca	exchangeable calcium
Ex-K	exchangeable potassium
Ex-Mg	exchangeable magnesium
Ex-Na	exchangeable sodium
Ext-P	extractable phosphorus
FIPI	Forest Inventory and Planning Institute
F_v/F_m	maximum quantum yield of photosystem II
GC	gap centre
GP	gap perimeter
g_s	stomatal conductance
H_t	top height
IUCN	International Union for Conservation of Nature
IVI	important value index
J_{max}	the potential rate of electron transport
LA	leaf area
LAD	leaf area density
LAI	leaf area index
L_b	branch length

L_{bg}	length of branch with green leaves
L_c	crown length
LUE	light-use efficiency
LZ	lower crown zone
MAI	mean annual increment
MARD	Ministry of Agriculture and Rural Development of Vietnam
MZ	middle crown zone
N_{leaf}	leaf nitrogen concentration
P	phosphorous
PAR	photosynthetically active radiation
P_{leaf}	leaf phosphorous concentration
R_{dark}	dark respiration
SD	standard deviation
SLA	specific leaf area
SOM	soil organic matter
TC	total organic carbon
TN	total nitrogen
UZ	upper crown zone
V_{cmax}	maximum rate of RuBP carboxylation
VPD_L	vapour pressure deficit based on leaf temperature
W_b	branch weight
W_l	leaf weight
W_s	stem weight
WUE_i	intrinsic water-use efficiency
θ_b	branch angle from stem
θ_l	leaf angle from horizontal line
Φ	apparent quantum yield
Ψ_{leaf}	leaf water potential
$\#_b$	number of live branches

Chapter 1

INTRODUCTION

1.1. Problem statement

After millions of years of relative stability, tropical forest ecosystems are in serious decline (Lamb, 2011b). This is associated with loss of biodiversity, greater vulnerability to changing climates and the potential extinction of many timber species. The catastrophic loss of mature trees because of overharvesting has meant lost capacity for regeneration and recovery owing to lack of seeds, and loss of receptive seedbeds as secondary forest occupies the space. Such high levels of disturbance also induce soil degradation and breakdown of forest structure, which themselves compromise regeneration. These accumulated impacts lead to the likelihood that restoration of the now degraded ecosystem by natural regeneration will become impossible (Lamb, 2011b).

There have been many attempts at reforesting degraded lands, and planting has been the preferred strategy (Lamb and Tomlinson, 1994). The ecological benefits that flow from such a strategy are questionable, particularly because these plantations are often monocultures and rely on a small number of planting species, mainly acacias, eucalypts and pines; these species are also exotic in most countries (Lamb, 2011a, b). The practice of establishing large areas of monocultures based on a clear-cutting silvicultural system also raises concerns about ecological conservation because of associated losses of biodiversity, genetic variation and sustainability (Kelty, 2006). A

compromise is to design plantations with structures more akin to natural forest that are multi-species and include native species, multi-storey and uneven-aged, and which in time can gradually recapture at least some of the ecological functions of the lost native forest. Lamb (2011b) stated that "mixed-species forests are not half-hearted attempts to mimic the diversity present in natural forests, but they do seek to take advantage of some of the functional advantages of the species-rich natural system, including their capacity to use resources more efficiently and to reduce nutrient losses from the system".

Re-establishment of native-tree species can also help to replace the high demand for quality timbers harvested from natural forests. While monoculture plantations of fast growing exotic species are well-suited to meeting the demand for low-value wood products and can also reduce pressure on the harvesting of natural forests for such products, they are mostly unsuitable as sources of high-value timber, and are rarely used in this way, especially in South-East Asian countries (Kammesheidt, 2011). The demand for quality timbers is associated with rising incomes and the scarcity of the species from which they are sourced in natural forests. This excess of demand over supply simply leads to a continuing increase in their market price, making them even more attractive for logging, both legal and illegal, hence the high rates of decline of natural forest resources. However, while substitution using planted native trees, such as the dipterocarp *Hopea odorata* Roxb., the focus of this study, may contribute to meeting this demand (Kammesheidt, 2011), the prospect of a long harvesting rotation of > 40 yrs is a major constraint for the growers, especially small-holders. A sustainable system for growers is a model that guarantees income but reduces the risk of ecological and environmental damage. Therefore, the plantation model should be diverse in species and technical treatments so as to provide diverse products and a diverse e.g. short-, medium-

and long-term income stream. A model which uses acacia as a nurse crop for supporting native-species plantation silviculture can partly meet this requirement.

Tropical *Acacia* species are commonly used for plantations. These species have high early growth rates, are adapted to harsh environments, and being legumes, can fix nitrogen (Binkley and Giardina, 1997; Brockwell *et al.*, 2005). In many countries, they have been used successfully as pioneer species for re-foresting and re-greening degraded landscapes (Peng *et al.*, 2005). A much less-successful use of acacia species as nurse crops for re-establishing native species in these landscapes has been recorded (Tam, 2007; Ren *et al.*, 2008). While monocultural plantations have been demonstrably successful, acacia nurse crops have been less so. This may be attributed to not fully understanding the site requirements of target native species and the potential for negative as well as positive between-species interactions in two- or multi-species plantations (Forrester *et al.*, 2005a; Ren *et al.*, 2008).

Site-species matching is essential for successful plantation establishment, and site requirements differ from species to species. The best way to find out about site requirements of a species is to learn from its natural habitat. However, different species also have different abilities to adapt to the new environments which are a common feature of plantations. For example, while many acacia and eucalypt species can adapt to site conditions quite unlike their natural habitat, hence their success as plantation species, many other native species have failed or have had less success when introducing into a different environment. Therefore, apart from investigating the preferred site conditions in its natural habitat, field-based experiments in a plantation context are also required to fully understand the range of site conditions under which the species can be grown.

As stated above, managing nurse-crop model as a mixed-species plantation is difficult due to a lack of understanding of their interactions. These are often related to how the species respond to the changes in environment experienced by each species as the plantation ages. In principle, mixed-species systems have productive advantages over monocultures, but in many situations mixtures offer no change or even a reduced productivity compared to monocultures (Forrester *et al.*, 2005a; Manson *et al.*, 2013). The failures of mixtures are often associated with asymmetric competition between species as the plantation develops (Manson *et al.*, 2013), for example competition for light is asymmetrical as taller plants shade smaller plants but not vice versa (Weiner, 1990; Forrester *et al.*, 2006). In addition, species respond differently to the changes of environmental variables. Some species can adapt to a wide range of light conditions without compromising their physiological performance, others cannot (Lee *et al.*, 2000). Thus, designing and managing successful mixtures need an understanding of ecological and physiological responses of the target species as the mixture develops.

To deal with the above issues in the context of using nurse crops for re-establishment of native-tree species (target species), we need to (1) examine the potential of matching the site requirements of the native-tree species with the site conditions created by nurse crops on degraded lands, and (2) understand how the target trees respond to the site conditions provided by nurse crops. Together this will lead to practical information for designing and managing these mixed-species plantations. The following issues need to be addressed by this thesis:

(1) What are the site requirements of native-tree (target) species?

(2) Are site conditions improved by the nurse crop and are its nurse effects adequate for establishment of the target-species plantations?

(3) How does the target species respond to the environments created by the nurse crop?

(4) How can the negative interactions be managed to maximise growth rate of the target trees?

This study selected *Hopea odorata* Roxb., a late successional dipterocarp species, as the target species, and *Acacia* hybrid, a fast growing and poor-site adapted clone of *A. mangium* × *A. auriculiformis*, as the nurse crop. The details of *A.* hybrid and *H. odorata* are provided in the literature review.

1.2. Objectives

The main objective of this study was to examine the potential of matching the site requirements of *H. odorata* with site conditions created by *A.* hybrid nurse crops on degraded lands. The specific focus was the response of *H. odorata* to the light, soil moisture and nutrient supply associated with the nurse crop. The results would provide practical information for designing and managing mixed-species plantations for the reintroduction of native timber species into the degraded landscape in Vietnam.

To fulfil this general objective, the specific objectives of this study were:

(1) To determine the site requirements of *H. odorata*

(2) To investigate how soil of degraded lands changes following establishment of short-rotation *A.* hybrid plantations

(3) To determine the physiological and growth responses of *H. odorata* to light and soil resources in association with an *A.* hybrid nurse crop

(4) To identify and propose management strategies to counter the negative interactions that may occur between *H. odorata* and a fast-growing nurse crop like *A.* hybrid

1.3. Outline of the thesis

This thesis consists of seven Chapters, an introduction, a literature review, four experimental chapters and a general discussion. The four experimental chapters are written in paper format as they have been, or are intended to be, submitted for publication. In brief:

Chapter 1: Introduction

An introduction to the problem and justification of the study approach.

Chapter 2: Literature review

A review of the relevant literature which identifies the important issues which need to be addressed in this research. The focus is the eco-physiological characteristics of *Hopea odorata* and the potential of *Acacia* species to act as nurse crops for native-tree plantation establishment in the tropics.

***Chapter 3: Site conditions for natural regeneration of* H. odorata**

An investigation of the site conditions for regeneration of *H. odorata* in its natural habitat, including stand structure, light and soil condition.

This chapter has been submitted and recommended for publication in the Journal of Tropical Forest Science with minor revision.

Chapter 4: Impact of short-rotation A. *hybrid plantations on degraded lands*

An examination of the potential for soil improvement by plantations of *A.* hybrid established on degraded lands. The differences of soil properties between 1 – 5 yr-old, second- or third-rotation plantations within a 5-yr rotation and abandoned lands are described.

Preliminary results from this chapter were presented at an Australian and New Zealand Soil Science Conference in December 2012, and published as:

Dong, T. L., Doyle, R. Beadle, C. L, Corkrey, R., 2012. Soil amelioration by *Acacia* hybrid: an assessment of soil condition for re-establishing native species in the tropics. In: *Soil Solutions for Diverse Landscapes*. 5th Joint Australian and New Zealand Soil Science Conference, Hobart, Australia, December 2012. Australian Society of Soil Science Incorporated.

This chapter has been published as:

Dong, T. L., Doyle, R., Beadle, C. L, Corkrey, R. and Quat, N. X., 2014. Impact of short-rotation *Acacia* hybrid plantations on soil properties of degraded lands in Central Vietnam. Soil Research 52, 271-281.

Chapter 5: Growth and physiology of* H. odorata *under nurse effects of* A. *hybrid plantations

A study of the growth and physiological responses of *H. odorata* seedlings to the site conditions created in circular gaps of a 3-yr-old *A.* hybrid plantation. The focus is the responses of *H. odorata* seedlings to the gradient of light availability and interspecific competition for below-ground resources. Physiological responses were examined through measurements of gas exchange, leaf water potential, leaf chemical, leaf pigment and structural traits.

Preliminary results from this chapter and Chapter 3 were presented at an international symposium on Tropical Forest Ecosystem Science and Management in September 2013, and published as:

Dong, T. L., Beadle, C. L., Doyle, R. and Worledge, D., 2013. Site requirements for re-establishment of *Hopea odorata* Roxb. on degraded lands. In: *Challenges and solutions*. 2nd International Symposium on Tropical Forest Ecosystem Science and Management, Bintulu, Malaysia, September 2013. Universiti Putra Malaysia.

***Chapter 6: Effects of light availability on crown structure, biomass production, light interception and light-use efficiency of* H. odorata**

An analysis of the responses of crown structure, biomass production, light interception and light-use efficiency to the gradient of light availability in circular and strip gaps of 3- and 2.5-yr-old, respectively, *A.* hybrid plantations. The MAESTRA model was used for estimating light interception.

Chapter 7: General discussion

A synthesis of the results in the context of matching site requirements of *H. odorata* planted in degraded landscapes in Vietnam with site conditions under *A.* hybrid nurse-crop plantations and their management, and some recommendations for application of the research findings in rehabilitation of degraded landscapes in Vietnam.

Degraded natural forests replaced by young *Acacia* hybrid plantations in Phong Dien district, Thua Thien Hue province. Photo: Tran Lam Dong, in May, 2011

Chapter 2

LITERATURE REVIEW

This chapter reviews the relevant literature to identify important issues that need to be addressed in the planned research. To start with, a lesson learnt from the 5M ha Reforestation Program in Vietnam (5MHRP) was used to identify the key issues for this review.

In 1998, Vietnam launched a huge national program that aimed to re-establish 5M ha of forest by 2010, 2M ha for protection of water resources and special-use forests and 3M ha for commerce (The Government of Vietnam, 1998). By 2011, 3.35M ha of new forest had been established. Of this, 0.9M ha was in the first category and included plantings aimed at restoring extensively degraded landscapes to native species (MARD, 2011). In his assessment of the silvicultural techniques applied to these 0.9M ha up to 2005, Tam (2007) commented as follows.

The typical model was a mixed planting of an acacia nurse crop with one or several indigenous species of potentially high ecological and economic value. Three nurse species, *A. auriculiformis* or *A. mangium* and their hybrid which is referred to here as "*Acacia* hybrid", and 36 indigenous species were represented in all ecological regions; *H. odorata* was one of the most popular target species. The standard design was 1000 acacia plus 600 indigenous trees per hectare. Row-by-row planting of the acacia and indigenous species led to higher early survival than strip plantings (2 – 3 rows acacia then 2 – 3 rows indigenous trees), possibly because of heavier shading in the former. However, after about three years, the acacia canopy had closed in the row-

by-row system and the native trees had become suppressed, stunted or had died. In spite of the lower early survival, trees grew better in the strip plantings after age 3 yrs. Overall, early survival rate of the native trees across the whole program after planting was between 81 – 97%. At age 3 yrs it was 60% on average, but as low as 25%. At the time of assessment, only 56% of the total area was considered viable mixed- native species plantations; the remainder only had acacia values. If no immediate treatment was applied, the percentage of mixed-species plantation was expected to decline further.

This happened in particular because of a poor understanding of site requirement and interactions between nurse and target species. Different species require different site conditions so one design is unlikely to work for all indigenous species. The best design combines species with niche differences in a way that reduces competition intensity (Matthew J, 1999; Kelty, 2006), and recognises that the site requirements of the target species may change with plant development, for example because of changes in the degree of asymmetric competition between species (Forrester *et al.*, 2006). In the 5MHRP, failure to manage competition for light was probably the crucial factor that resulted in poor outcomes. The demand for light of the shade-tolerant target species almost certainly changed as the trees grew. While shading during seedling establishment enhanced survival (Norisada *et al.*, 2005; Yang *et al.*, 2009), once established, heavy shading by the nurse crop had the opposite effect (McNamara *et al.*, 2006). In mixed plantations of 16 – 18-yr-old *A. auriculiformis* and 7-yr-old *H. odorata* and *D. alatus* in Central Vietnam, growth rates of the target trees increased with decline of the relative number of nurse-crop trees; *H. odorata* had the best growth rate at 30% full sunlight (McNamara *et al.*, 2006). Similarly, height and DBH increment of 68-month-old *Anisoptera marginata*, a dipterocarp species, planted under 80-month-old *A.*

mangium increased with the degree of opening of the canopy gaps (Otsamo, 1998b). Otsamo (2000a) demonstrated a distinct relationship between light availability and growth of three 19-month-old dipterocarp species planted in artificial gaps of 5-yr-old *A. mangium*. The author concluded that stand manipulation either by opening gaps or by other methods to facilitate the growth of understorey trees was essential when using nurse crops that produce heavy shading (Otsamo, 2000a).

From the above lesson, the review will focus on the eco-physiological characteristics of *Hopea odorata* in order to understand its ecological requirements and adaptation to environment. It will also examine the potential of *Acacia* species to act as nurse crops for native-tree plantation establishment in the tropics. The focus will be on *Acacia mangium* and *A. auriculiformis*, and *A.* hybrid; all three have been exploited for monocultures and as nurse crops. The success or otherwise of nurse-crop systems in other contexts will also be examined and used to propose strategies for this research which aims to increase the success rate for the re-introduction of native species under tropical acacias.

2.1. Eco-physiology of *Hopea odorata* Roxb.

Hopea odorata is a late successional dipterocarp which is naturally distributed in many South-east and South Asian countries, including Vietnam (PROSEA Foundation, 1993; Hong, 2012). It is a large evergreen tree which can reach 45 m tall, with a straight, cylindrical, branchless bole up to 25 m, and stem diameter of up to 120 cm or more (PROSEA Foundation, 1993). Its timber is highly valued because of its durability and

resistance to insects, and use for weight-bearing construction (PROSEA Foundation, 1993). Due to over-logging in the past, *H. odorata* is currently assessed as vulnerable in the International Union for Conservation of Nature (IUCN) "Red List" of threatened species (IUCN, 2012). In Vietnam, it has been listed as a priority species in need of immediate conservation (Hong, 2012).

Research on planting of *H. odorata* began early in the 20th century, but was only carried out more widely during last 30 yrs, mainly in Bangladesh, Cambodia, India, Indonesia, Nepal, Malaysia, Philippines, Thailand, and Vietnam (Weinland, 1998). Although ecology, physiology and silviculture have been widely studied, successful plantations of *H. odorata* as well as other dipterocarps are mainly experimental trials; very little success has been reported from reforestation programs, except for some urban plantings (Weinland, 1998). Being considered a shade-tolerant species, the most common approaches to its establishment have been enrichment planting and planting with nurse crops for either timber or conservation (Weinland, 1998). In Vietnam, it has been a major species in reforestation programs, but many have failed because of the use of inappropriate planting sites and silvicultural treatments (Tam, 2007). Successful plantations can achieve a mean annual increment (MAI) of 7.5 – 13.3 m^3 ha^{-1} (Que *et al.*, 2010).

The objective of this study is to examine the potential of *H. odorata* for re-establishment on the degraded lands. Site species matching is essential for successful establishment. Information on site requirements can be obtained through investigation of the habitat where the species grows naturally, and validation through experimental trials. The morphological and physiological responses when adapted to new environments provide important information for plantation management. This section

reviews secondary data which are related to the ecological requirements of *H. odorata* and its responses to environment.

2.1.1. Taxonomy

Dipterocarpaceae is an important family in the South-east and South Asian countries. The family consists of three subfamilies with approximately 500 species in 17 genera (Ashton, 1982; Rath *et al.*, 1998; Dayanandan *et al.*, 1999; Choong *et al.*, 2008). The largest subfamily Dipterocarpoideae comprises about 470 species in 13 genera, in which *Hopea*, the second largest genus after *Shorea*, contains 102 species (Ashton, 1982; PROSEA Foundation, 1993). According to Ashton (1998), *H. odorata* belongs to: Kingdom: Plantae; Phylum: Tracheophyta; Class: Magnoliopsida; Order: Theales; Family: Dipterocarpaceae; Species: *Hopea odorata* Roxb.

2.1.2. Geographical and ecological distribution

The genus *Hopea* Roxb. is distributed from mainland South-east Asia to Peninsular Malaysia, Sumatra, Borneo, the Philippines and New Guinea (PROSEA Foundation, 1993). It is found from sea-level to 1650 m altitude, occurring as a main canopy or understorey but rarely as an emergent tree in evergreen and semi-evergreen forests. The different species in this genus appear in a wide variety of forest types including mixed dipterocarp, heath, and swamp forests (PROSEA Foundation, 1993).

Hopea odorata is native to the Andaman Islands, Bangladesh, Cambodia, Laos, Malaysia, Myanmar, Thailand, and Vietnam (PROSEA Foundation, 1993). It is a riparian species usually occurring in evergreen mixed dipterocarp forests ranging from

sea-level to 600 m altitude (PROSEA Foundation, 1993; Bunyavejchewin *et al.*, 2003). In Vietnam, it is naturally distributed in the South-east, South Central Coast and Central Highlands regions, ranging from 10.5^{o} – 15^{o} N and 106^{o} – 109^{o} E, and from sea level to 750 m altitude (Hong, 2012). Mean temperature and annual rainfalls in these areas range from 25 – 30^{o} C and 1500 – 2500 mm, respectively. This species is widely geologically adapted, and was successfully planted further north up to latitude 21.5^{o} N (Hung *et al.*, 2010).

2.1.3. Ecological requirements

2.1.3.1. Light

Under natural conditions, regeneration occurs where there is shade, suggesting that seedlings are adapted to shady conditions (Sakai *et al.*, 2009). Shade-house experiments showed that growth rate and physiological performance of seedlings were highest in between 10 – 40% of incident photosynthetically active radiation (PAR) (Lee *et al.*, 1997; Lee *et al.*, 2000). In plantations, previous studies found that shading benefits settlement and early growth of *H. odorata* seedlings, which leads to high survival rates and avoidance of photoinhibition with sudden changes to high irradiation conditions (Norisada *et al.*, 2005). However, at later ages, growth rate declines under heavily shading by nurse species like *Acacia* and *Eucalyptus* (McNamara *et al.*, 2006; Sakai *et al.*, 2009); continuous shading can compromise survival (Kamaluddin and Grace, 1993). This was also found in some other dipterocarps species (Nicholson, 1960; Otsamo, 2000a; Ashton *et al.*, 2006).

Although *H. odorata* seedlings are considered as shade-tolerant, it can acclimatise to high light conditions (Lee *et al.*, 1997; Lee *et al.*, 2000). Under full sunlight, photosynthetic rate of *H. odorata* was not significantly different compared to shading treatments (Lee *et al.*, 1997), but biomass production was highest because of higher receipt of radiation (Phonguodume *et al.*, 2012).. Such acclimatisation indicates that the physiological traits of leaves change to adapt to high irradiation, and leaf traits become closer to those of sun plants e.g. thicker leaves and lower chlorophyll content, particularly chlorophyll b (Lee *et al.*, 2000). This enables leaves to have higher photosynthetic rate (A_{max}) which are associated with higher stomatal conductance (g_s) and dark respiration (R_{dark}) (Lee *et al.*, 1997). However, a lower rate of biomass production per unit of light (mg mol^{-1}) was found this treatment, again a common finding in sun *v.* shade plants (Lee *et al.*, 1997). Photo-damage may happen to shade-tolerant plants when exposed to high irradiation and this was observed for *H. odorata* by Norisada *et al.* (2005)

In plantations with nurse crops, growth rates of *H. odorata* may be insufficient for successful establishment, but other benefits need to be taken into account. Other performance indicators such as survival rate, vigour, morphology and stem form may also be affected by light conditions (Weinland, 1998). Without shading, survival rate of the dipterocarp seedlings were significantly lower (Norisada *et al.*, 2005; Sakai *et al.*, 2009) and poorer stem form due to dieback of the top of seedlings (Lee *et al.*, 1997; Norisada *et al.*, 2005). In addition, shading by nurse crops is good for weed control (Otsamo, 1998a). As growers want to maximise biomass from the limited space available, mixed species cropping with nurse species may enhance total biomass production through better use of incident light.

2.1.3.2. Soil

a) Soil type

Hopea odorata naturally grows in seasonal dry evergreen dipterocarp forests and is typically found on the lower lying and flatter areas. This suggests it prefers deeper soils with higher moisture supply (Bunyavejchewin *et al.*, 2003). Suitable substrates vary from well-drained clayey soils to sandy soils, alluvial soils, podzols (leached sandy acidic soils), swampy soils or peats (PROSEA Foundation, 1993). In Thailand, soils in seasonal dry evergreen dipterocarp forests are developed from deeply weathered granite, shale, sandstone, mudstone, conglomerate, and volcanic tuff, and typical soils are classified as clayey Oxisols (Bunyavejchewin *et al.*, 1998). In lowland and hill dipterocarp forests in Peninsular Malaysia, soils are developed from sandstone and granite slope-wash with soil textures ranging from sandy clay loams to sands; soil types are typically classified as Inceptisols and Ultisols (Zaidey *et al.*, 2010). In mixed dipterocarp forests in North-western Borneo, soils are developed from sandstone, basalt, shale, dacite, and rhyolite, and soil texture ranges from clay to sandy; soils are classified as Humult/Udult-Ultisol, Oxisol, and Inceptisol (Ashton and Hall, 1992). Soils in mix dipterocarp forests in Lambir, Sarawak are developed on sandstone and shale, with texture ranging from clay to sandy loam; soils are classified as Arenic-, Ferralic- and Haplic-Acrisols (Baillie *et al.*, 2006; Russo *et al.*, 2007). Although soil types of evergreen dipterocarp forests are highly varied, *H. odorata* may not always present over all these areas and soil types, because the primary factors controlling establishment of natural *H. odorata* populations require soil moisture and flat to low lying topography (Bunyavejchewin *et al.*, 2003).

b) Soil nutrient and other properties

Secondary evergreen dipterocarp forests are found in environments with low to high soil nutrient concentrations (Ashton and Hall, 1992; Grubb *et al.*, 1994; Baillie *et al.*, 2006; Paoli *et al.*, 2006; Zaidey *et al.*, 2010). This suggests dipterocarp species can adapt to a wide range of soil conditions. However, significant relationships between species distribution (Paoli *et al.*, 2006), diameter and height (Ashton and Hall, 1992), physiological performance (Norisada and Kojima, 2005) and some key nutrients, particularly N, extractable P and Mg, indicate an effect of nutrients on seedling recruitment and tree growth. *Hopea odorata* is in a moderate growth-rate group, and there are some evidences that the species can adapt on soils with poor nutrient levels. In Vietnam, it has been widely planted on degraded lands where soil nutrient levels are low, but this was not a constraint on growth; mean annual increments (MAI) were 7.5 – 13.3 m^3 ha^{-1} (Que *et al.*, 2010). Nutrient requirement may depend on the availability of light or soil moisture. In low light environments such as in gap and closed dipterocarp forest, fertilising effects on dipterocarp seedling growth were low (Turner *et al.*, 1993), however, the demand for nutrients may increase in non-limiting light environments, presumably to support higher growth rates (Nussbaum *et al.*, 1995). Under well-watered treatments, *H. odorata* growth rates differed with fertiliser supply; seedlings grew best in the media containing 0.16% N, 0.034% P and 0.032% K, although differences between treatments were smaller in water-stress treatments (Zainudin *et al.*, 2003).

Nitrogen was found to be important not only for the overall growth of dipterocarps but also for enhancing photosynthetic rate and avoiding photodamage (Bungard *et al.*, 2000). Under high irradiation, photosynthetic rate of seedlings in the high N-supply treatment were significantly greater than the low N-supply treatment, but

not significantly different under low irradiation. Photodamage (decline of F_v/F_m) was related to light environment and nitrogen availability. Seedlings grown under low irradiation and low N had greater photodamage when exposed to high irradiation than seedlings in the high N treatment (Bungard *et al.*, 2000). Growth and photosynthetic rate of *H. odorata* was significantly higher under ammonium than nitrate fertiliser treatment (Norisada and Kojima, 2005). This may be an advantage for *H. odorata* when growing with acacia nurse crops, as the dominant form of nitrogen fixed is ammonium.

Acidic soils (pH_{H2O} as low as 4.2) are found in secondary evergreen dipterocarp forests (Ashton and Hall, 1992; Grubb *et al.*, 1994; Baillie *et al.*, 2006; Paoli *et al.*, 2006; Zaidey *et al.*, 2010). Slightly to strongly acidic soils are not related to dipterocarp species distribution, indicating that soil acidity has little effect on tree growth (Ashton and Hall, 1992; Paoli *et al.*, 2006). Vigorous growth of *H. odorata* plantations in Vietnam under acidic soil conditions (pH_{KCl} = 3.9 – 4.7) suggests the species is well-adapted to low soil pH (Que *et al.*, 2010).

Soil compaction can impair rooting behaviour at germination (Dabral *et al.*, 1984; Zainudin, 2000) and seedling growth (Nussbaum *et al.*, 1995) of *H. odorata* and other dipterocarps. However, while a BD >1.6 g cm^{-3} significantly restricted rooting of three-month-old *H. odorata*, there was no significant effect when seedlings were over six months old, suggesting adaptation to soil compaction (Zainudin, 2000).

c) Soil moisture

In nature, *H. odorata* usually grows in riparian and evergreen moist forests. It is often found near streams and in swampy sites, and stand density is highest on the lowest and

flattest sites (Bunyavejchewin *et al.*, 2003). Previous studies have shown higher growth rates for seedlings in well-watered (at field capacity ≥ –0.3 MPa) *v.* water-limited treatments (only watering to field capacity when soil water potential is as low as –1.5 MPa) (Zainudin *et al.*, 2003). Even water-logging for up to 60 days did not affect the physiological performance of *H. odorata* seedlings (Abdul-Hamid *et al.*, 2009). Competition for water may constrain growing *H. odorata* in mixtures with fast-growing nurse crops such as acacias (Norisada *et al.*, 2005) as these species have a high consumption and storage of water (Cienciala *et al.*, 2000; Yamamoto *et al.*, 2003; Inagaki *et al.*, 2008; Wang *et al.*, 2011) .

2.2. The potential of using *Acacia* species as nurse crops

2.2.1. *Acacia* as a pioneer species

2.2.1.1. Why use Acacia *in reforestation?*

Species with fast early growth rates and adaptation to degraded soils such as tropical acacias, eucalypts and pines are usually selected as pioneer species for re-greening degraded landscapes (Yang *et al.*, 2009). In the tropics, despite the huge benefits brought to growers, eucalypts have been associated with rapid depletion of water and nutrients, vigorous competition with local vegetation, and allelopathic effects on native flora and fauna, thereby lowering biodiversity (Casson, 1997). Pines have also been reported to inhibit the regeneration of other species, partly due to their own strong ability for natural regeneration (Kasel, 2004), which again lowers biodiversity. Although tropical *Acacia* species, including *A. mangium* and *A. auriculiformis* and their

natural hybrid have also been labelled as invasive (Kotiluoto *et al.*, 2009; Le Maitre *et al.*, 2011; Morris *et al.*, 2011; Richardson *et al.*, 2011), they have received better acceptance because of their tolerance and adaptation to a wide range of sites and their ability to fix atmospheric nitrogen and improve soil fertility (Cole *et al.*, 1996; Binkley and Giardina, 1997; Brockwell *et al.*, 2005). Therefore, acacias are usually selected as pioneer or nurse species in reforestation for landscape recovery (Turnbull *et al.*, 1998; Peng *et al.*, 2005; Nichols and Carpenter, 2006). With at least similar growth rate and wood quality to eucalypt and pine, but there also being a huge market for their wood products, acacias have become the preferred species in Vietnam. Two species, *A. auriculiformis* and *A. mangium* are the most often used for re-forestation; however their natural hybrid is dominant in Vietnam (Kha, 2001).

a) Acacia auriculiformis

Native populations of *A. auriculiformis* are found in lowland areas of north Queensland and the north of the Northern Territory of Australia, Central and Western Provinces of Papua New Guinea (PNG), and Irian Jaya and the Kei Islands of Indonesia, ranging from 5 – 17^{o} S and 130 – 148^{o} E, and from near sea level to 400 m altitude (Boland *et al.*, 1990; Doran and Turnbull, 1997).

The species has been grown in Malaysia, Thailand, the Philippines, India, China and Vietnam for >50 yrs, where it is well-known to be adapted to poor sites (Turnbull *et al.*, 1998; Phi Hong Hai, 2009; Griffin *et al.*, 2011). It can grow on sandy to heavily clay soils, soils from pH 4.3 – 8.0 (Doran and Turnbull, 1997), annual rainfall between 450 mm in Australia (Doran and Turnbull, 1997) and 3400 mm in PNG (Boland *et al.*,

1990). These properties made it a widely planted species to assist the recovery of degraded landscapes in South-east Asian countries, China and India (Turnbull *et al.*, 1998; Brockwell *et al.*, 2005; Peng *et al.*, 2005). However, because *A. auriculiformis* is more resistant to stem degrade, root rot and heart rot than *A. mangium*, there has been more focus on improvement of this species to produce superior clones for solid-wood products; clones have already been released for commercial planting in Vietnam and Thailand (Turnbull *et al.*, 1998; Phi Hong Hai, 2009). There are few official statistics about the current plantation area by country; some recent estimates indicate 90,000 ha in Vietnam (Nambiar and Harwood, 2014) and 100,000 ha in India (Griffin *et al.*, 2011).

b) Acacia mangium

Acacia mangium is naturally distributed in tropical lowland areas in northern Queensland, Australia, western PNG and eastern Indonesia ranging from 1^{o} – 19^{o} S latitude, 125^{o} – 146^{o} E longitude and majorly from near sea level to about 300 m, but found up to 780 m altitude (Doran and Skelton, 1982; Pinyopusarerk *et al.*, 1993; Midgley and Turnbull, 2003). It prefers a humid climate and >1000 mm rainfall (Midgley and Turnbull, 2003).

The potential of this species to tolerate a wide range of environments and its use for landscape restoration was first recognised over 40 yrs ago when it was first introduced to Sabah for restoration of *Imperata cylindrica* grasslands (Doran and Skelton, 1982). It was then introduced for the same purpose to South Sumatra, China, and Vietnam in the early 1980s for restoration of degraded land (Turnbull *et al.*, 1998). It is well-adapted to degraded, sandy and acidic soils with pH <4.0 (Tilki and Fisher,

1998; Midgley and Turnbull, 2003; Norisada *et al.*, 2005; Yang *et al.*, 2009). Its fast growth rate even on poor soils made it become a major commercial plantation species for pulpwood, solid wood and plywood, particularly in Indonesia and Vietnam (Turnbull *et al.*, 1998; Arisman and Hardiyanto, 2006), and has been introduced to many countries in South and South-east Asia, Africa and Central and South America (Griffin *et al.*, 2011). In Vietnam, where *A. auriculiformis* and *Acacia* hybrid are also widely planted, *A. mangium*, with an estimation of 600,000 ha in Vietnam (Nambiar and Harwood, 2014), is selected for growth rate over the former and for its resistance to strong wind and typhoon events over the latter. It has gained particular preference in northern Vietnam.

c) Acacia hybrid

Acacia hybrid is a naturally occurring hybrid between *A. mangium* × *A. auriculiformis*. It was first recorded by Hepburn and Shim in Sabah, Malaysia in 1972 and identified as a hybrid of the two parental species by Pedley in 1978 (Pinso and Nasi, 1991). In Vietnam, it was first observed in the early 1990s by Le Dinh Kha (Kha, 2000). Recognised for superior traits inherited from its parents, an intensive program of clonal selection has been carried out by Vietnamese Academy of Forest Science (VAFS) in cooperation with CSIRO. Commercial clones were released in 1996 (Bueren, 2004).

Acacia hybrid was quickly adopted by forest growers in Vietnam because of its fast growth and wide adaptation to degraded sites. Its mean annual increment (MAI) can be >30 m^3 ha^{-1} yr^{-1} on good sites and generally exceeds that of its parents (Kha, 2001; Bueren, 2004). It can be grown in most lowland areas in Vietnam, especially in central

and southern areas, on degraded soil with pH_{KCl} as low as 3.5, on a wide range of sandy to clay soils, and in loose and compacted soil (Que *et al.*, 2010).

Acacia hybrid is currently one of the dominant species for commercial planting in Vietnam; the area is estimated to be about 400,000 ha (Nambiar and Harwood, 2014). The major product is pulpwood with a small portion of saw log in a cutting rotation of about five years. The major concern from forest growers in Vietnam is its low resistance to strong winds and typhoons, and susceptibility to heart rot which may compromise its use for solid-wood products over longer rotations (Tran Thanh Trang, pers. comm.).

2.2.1.2. Soil changes under acacia plantations

a) Soil chemical properties

1) Soil organic matter (SOM)

Soil organic matter including "all organic materials found in soils irrespective of origin or state of decomposition" (Baldock and Skjemstad, 1999) is an essential reservoir for soil fertility (Craswell and Lefroy, 2001). Decomposition of SOM releases soil nutrients for plant uptake and enhances soil fertility. SOM is composed of C, H, O, N, P and S, so it is difficult to measure. The most common method is to determine the soil organic carbon (SOC) content and estimate SOM through a conversion factor called the van Bemmelen factor, where usually SOC is taken as 58% of SOM (Attiwill and Leeper, 1987; Howard and Howard, 1990; Baldock and Skjemstad, 1999; Krull *et al.*, 2004).

Plantations of *A. mangium* and *A. auriculiformis* show significantly greater enhancement of SOC than other plantation species (Table 2.1). Legume tree species can

deposit up to 12 Mg dry litter ha^{-1} yr^{-1} (Franco and De Faria, 1997). For *A. mangium*, rates of deposition of 9.4 to 11.1 Mg ha^{-1} yr^{-1} (Li *et al.*, 2000; Hardiyanto and Wicaksono, 2008), and for *A. auriculiformis* of 4.8 to 6.7 Mg ha^{-1} yr^{-1} (Li *et al.*, 2000; Huong *et al.*, 2008), have been recorded. There is a wide variation of SOC between sites (Table 2.1). This variation is associated with soil type and climate (Baldock and Skjemstad, 1999; Krull *et al.*, 2004). In sandy and clay soils, steady state values of SOC are around 1 – 1.5% and 3.5 – 4.4%, respectively (Körschens *et al.*, 1998); both are associated with productive acacia plantations.

Site management is crucial for the maintenance of SOM stocks. Silvicultural systems based on acacia monocultures and clear cutting can trigger losses of SOM, soil organisms and soil function (Macedo *et al.*, 2008). Following afforestation, SOM levels in the surface typically decrease during the first five years and then recover to the pre-afforestation levels or become slightly higher (Paul *et al.*, 2002; Norisada *et al.*, 2005). Disturbance caused by land preparation for new planting is the major reason for this decline (Paul *et al.*, 2002), in part because the exposed SOM is vulnerable to erosion by rain and wind. In addition, wood harvesting removes a considerable amount of nutrients from the commercial parts of plantation (Hardiyanto and Wicaksono, 2008; Huong *et al.*, 2008). In Vietnam and elsewhere, burning slash and litter after harvesting to reduce land preparation costs is still prevalent, which can lead to the loss of a substantial amount of SOM (Huong *et al.*, 2004; Hardiyanto and Wicaksono, 2008). Silvicultural systems which limit exposure of land and retain litter and residues after harvesting are more suitable for maintaining SOM stock.

Table 2.1 Total SOC content (%) in plantations of some acacia species in comparison with some other species and land-use types

Site condition and location	Age (yr)	SL (cm)	*Am*	*Aa*	*E*	OS	GL	Reference
– Degraded soil, South China	24	0 – 20	2.11	1.56			1.28	(Yang *et al.*, 2009)
– Degraded soil, South China	23	0 – 10	5.58	5.51	4.02	3.195 *mixed natives*	4.06 *Shrub-land*	(Wang *et al.*, 2010a)
– Sandy savannah soil, Congo	6 – 7	0 – 10	0.70	0.71	0.71	0.59	0.73	(Bernhard-Reversat,
	7 – 9	0 – 10	0.93	0.92	0.71	*10-yr pine*	*savannah*	1996)
– Degraded sandy soil, Thailand	3.5	0 – 3	1.90					(Norisada *et al.*, 2005)
– Clay extracted area, Brazil	3	0 – 20	2.94		1.86		2.47	(Schiavo *et al.*, 2009)
– Poor to good soil in S. Sumatra, Indonesia	2 – 5.5	0 – 20	1.38 – 4.7					(Nurudin, 2007)
– South Kalimantan, Indonesia			1.47 – 2.21					(Simpson, 1992)
– Sandy soil, Congo	4	0 – 25		1.16			0.86	(Kasongo *et al.*, 2009)
		25 – 50		1.03			0.77	
	10	0 – 25		1.94			0.86	
		25 – 50		1.00			0.77	
	17	0 – 25		2.92			0.86	
		25 – 50		1.31			0.77	

SL: Soil layer; Am: *Acacia mangium*; Aa: *Acacia auriculiformis*; E: Eucalypt; OS: Other species; GL: Grassland.

2) Nitrogen (N)

Because of their N_2-fixation ability, acacias are anticipated to increase N content in soil. Annual deposition of N from acacia plantation is up to 200 kg N ha^{-1} yr^{-1} (Binkley and Giardina, 1997; Forrester *et al.*, 2006). The range observed for *A. mangium* is from 55 to 157 kg N ha^{-1} yr^{-1} (Bernhard-Reversat, 1996; Galiana *et al.*, 2002; Yang *et al.*, 2009), and 140 kg N ha^{-1} yr^{-1} for *A. auriculiformis* (Bernhard-Reversat, 1996; Kasongo *et al.*, 2009; Yang *et al.*, 2009).

Plantations of *A. mangium* and *A. auriculiformis* show significantly greater enhancement of soil N than other plantation species (Table 2.2). This originates mainly from high concentrations of N in litter deposits and root exudates (Brockwell *et al.*, 2005; Forrester *et al.*, 2006). The N content of acacia litter is four to seven times higher than for eucalypts and pines (Bernhard-Reversat, 1996; Bouillet *et al.*, 2008). Decomposition of this rich N litter releases a high amount of N to soils. This ability makes acacia species attractive for inter-planting with non-legume species (Bouillet and Bernhard-Reversat, 2001; Brockwell *et al.*, 2005; Forrester *et al.*, 2006). A review of 18 studies of plantings of N_2-fixing species with eucalypts indicated that the N content in litter-fall and soil of the mixed-species plantations was significantly higher than in the single-species eucalypt plantations; this eventually led to higher productivity in many cases (Forrester *et al.*, 2006).

There remain uncertainties in our understanding of the relative N_2-fixing ability of tropical acacia species and their capacity to change soil N. Yang *et al.* (2009) reported that N in soils under *A. mangium* was greater than that under *A. auriculiformis*; conversely Bernhard-Reversat (1996) reported higher N in soils under *A. auriculiformis*, though the growth rate of the *A. mangium* was higher. Nodulation (Sun *et al.*, 1992a) and nitrogenase

activity (Sun *et al.*, 1992b), essential parts of the N_2-fixation process, can vary significantly among acacia species and provenances within a species like *A. mangium* (Sun *et al.*, 1992a; Sun *et al.*, 1992b). In addition, temperature, soil moisture stress, soil salinity and available soil nutrients, especially phosphorus (P), modify rates of N fixation (Serraj and Adu-Gyamfi, 2004; Brockwell *et al.*, 2005). Tests on five African acacia species in Sudan by Habish (1970) found that the most effective nodulation was at 30-35^{o}C; it ceased when soil temperature was >40^{o}C; nodule and plant dry mass was optimum at 15% soil moisture. Phosphorus deficiency may limit nodule growth or nitrogenase activity (Sun *et al.*, 1992a; Vadez *et al.*, 1995; Ribet and Drevon, 1996). N_2-fixation activity also depends on symbiotic bacterial strains (Zahran, 1999). In a comparison of ten *Rhizobium* strains and 13 acacia species, Dreyfus and Dommergues (1981) found that host-species and *Rhizobium* strain combinations varied from zero to highly-effective nodulation. N_2-fixing ability also changes seasonally. In southern China, Peng *et al.* (2005) observed that nodules are usually formed in April when nitrogenase activity was 0.08 μmol C_2H_4 g^{-1} fresh nodule h^{-1}; peak activity was in July (5.84 μmol C_2H_4 g^{-1} fresh nodule h^{-1}) and they were moribund by November. All these studies suggest a potential for improving N_2-fixation ability of acacia through selection at species, provenance and symbiotic strain levels; site should ensure adequate P supply.

Table 2.2 Soil N content (%) in plantations of some acacia species in comparison with some other species and land-use types

Site condition and location	Age	SL (cm)	*Am*	*Aa*	*E*	OS	GL	Reference
– Degraded soil, South China	24	0 – 20	0.103	0.092			0.067	(Yang *et al.*, 2009)
– Degraded soil, South China	23	0 – 10	0.104	0.092	0.082	0.081 *mixed natives*	0.082 *shrub-land*	(Wang *et al.*, 2010a)
– Sandy savanna soil, Congo	6-7	0 – 10	0.046	0.05	0.042	0.037 *10-yr pine*	0.046 *savanna*	Bernhard-Reversat, 1996)
	7-9	0 – 10	0.058	0.059	0.04			
		10 – 20		0.04	0.028		0.04	
		20 – 40		0.03	0.023		0.03	
		40 – 60		0.027	0.029		0.03	
– Degraded sandy soil, Thailand	3.5	0 – 3	0.09					(Norisada *et al.*, 2005)
– Clay extracted area, Brasil	3	0 – 20	0.202		0.164		0.104	(Schiavo *et al.*, 2009)
– South Sumatra, Indonesia	2 – 5.5	0 – 20	0.08 – 0.28					(Nurudin, 2007)
– South Kalimantan, Indonesia			0.104 – 0.144					(Simpson, 1992)
– Sandy soil, Congo	4	0 – 25		0.08			0.045	(Kasongo *et al.*, 2009)
		25 – 50		0.08			0.04	
	10	0 – 25		0.186			0.045	
		25 – 50		0.08			0.04	
	17	0 – 25		0.28			0.045	
		25 – 50		0.10			0.04	

SL: soil layer; *Am*: *Acacia mangium*; *Aa*: *Acacia auriculiformis*; *E*: Eucalypt; OS: other species; GL: Grass land.

3) Phosphorus (P)

Walker and Adams (1958) stated that "biological N-fixation would cease under natural conditions when available P had disappeared and non-N_2-fixers were competing successfully for all the N and P being mineralised from soil organic matter" (Walker and Syers, 1976). This statement is based on the principle that P is an essential ingredient for symbiotic bacteria to convert atmospheric N_2 to the usable NH_4 form for plant and microbial uptake. This is because the bacteria need a high P content to provide energy (ATP) for nodule development and the nitrogenase reaction (Sprent and Raven, 1985). This is reflected by a high P content in nodules, ranging from similar to double that of leaves (Hart, 1989; Sprent, 1999). However, as the fraction of nodule dry weight in total plant dry weight is about 5%, the fraction of P nodule content in total plant P is small (Sprent, 1999). Nevertheless, the importance of P for acacia needs to be fully examined.

For acacia, P is important for nodule development. Nodule growth of 36-week-old inoculated *A. mangium* seedlings increased with increasing supply of P (Ribet and Drevon, 1996). Similar results have been obtained elsewhere with *A. mangium* (Sun *et al.*, 1992a; Vadez *et al.*, 1995) and *A. auriculiformis* (Sun *et al.*, 1992a). In some instances, the effect of P on nitrogenase activity of acacia showed similar behaviour (Sun *et al.*, 1992b; Vadez *et al.*, 1995). However, this activity also increased with P deficiency treatments in *A. mangium* as a result of higher allocation of P to the nodule than to the leaves (Ribet and Drevon, 1996). This may be because of differing between-species or between-provenance tolerance to P stress (Sun *et al.*, 1992a) through their ability to utilise internal P (Ribet and Drevon, 1996). Strains of rhizobia can also vary in their tolerance to P stress, especially under acidic conditions (Zahran, 1999). The efficient utilisation of internal P by either host or rhizobium enables adaptation in P deficient environments (Ribet and Drevon, 1996;

Sprent, 1999). These make acacias are well-adapted to soils with low P levels as low as 0.2 ppm in *A. mangium* (Vadez *et al.*, 1995).

For plant growth, P is only important when their N requirement is satisfied. A common method for testing the dependence of legume trees on P availability is to observe the interaction of plant growth to fixed N only or supplementary N at different levels of P supply (Robson, 1983). During the first 12 weeks, N-fed plants grew faster than N_2-fixing plants in all P treatments because of N deficiency in the N_2-fixing treatment (Ribet and Drevon, 1996). This is because nodules only appeared 4 – 6 weeks after transplanting; consequently the effect of P on plant growth only appeared after 10 weeks. After 22 weeks, growth rates were similar in both sources of N and there was a significant increased with increasing P supply to an optimal level (Ribet and Drevon, 1996). At higher levels, inhibition symptoms can develop (Sun *et al.*, 1992a). Thus, while P is crucially important for nodule development, N is more critical for plant growth.

High soil acidity level influences soil P availability; the optimum pH is between 6.0 to 7.0 (Armstrong and Griffin, 1999). Soils in tropical acacia plantations are usually acidic with a high content of iron and aluminium oxides (Kasongo *et al.*, 2009), elements that can easily process soluble P into insoluble compounds (Shen *et al.*, 2011). This inevitably limits the uptake of P fertiliser. As it is fixed, little P is lost to leaching, and it will be slowly released in soluble form at a later date (Griffith, 2001).

Tropical acacias are expected to promote the recovery of soil P because of their fast growth and short nutrient cycle. From the limited information available, total soil P ranged from 0.009 – 0.06% in *A. mangium* and was 0.015% in a *A. auriculiformis* plantation; extractable P ranged from 2.2 – 9.0 mg kg^{-1} soil in *A. mangium* and 3.6 mg kg^{-1} in *A.*

auriculiformis (Table 2.3). For reforestation of degraded land, acacia plantations result in significantly higher total soil P than eucalypts (Schiavo *et al.*, 2009; Wang *et al.*, 2010a), pines (Jeddi *et al.*, 2009), monoculture and mixed native-species plantations (Wang *et al.*, 2010a) and open sites and grassland (Schiavo *et al.*, 2009; Yang *et al.*, 2009).

Table 2.3 Soil P content (%) in plantations of some acacia species in comparison with other species

Site condition and location	Age	SL (cm)	Total P (%) / Extractable P (mg/kg)				Reference
			Am	*Aa*	*E*	GL	
– Degraded soil, South China	24	0-20	0.024 4.667	0.015 3.600		0.015 1.367	(Yang *et al.*, 2009)
– S. Kalimantan, Indonesia		N/A	0.008 – 0.056 2.2 – 9.0				(Simpson, 1992)
– Clay extraction area in Brasil	3	0-20	0.0011		0.0009	0.0008	(Schiavo *et al.*, 2009)

SL: soil layer; *Am: A. mangium*; *Aa: A. auriculiformis*; *E: Eucalypt*; GL: Grassland

4) Exchangeable cations (K^+, Na^+, Ca^{2+} and Mg^{2+})

Their high rates of deposition of organic matter mean that planted acacias can lead to increases in exchangeable cations. In an *A. auriculiformis* plantation on sandy soil in the Congo, the sum of exchangeable cations increased between age one and 17 yrs; the largest changes were in Ca^{2+} and Mg^{2+} at age 10 yrs; K^+ and Na^+ did not change much as they are more easily leached on sandy soil (Kasongo *et al.*, 2009) (Table 2.4). *Acacia mangium* was associated with more exchangeable cations than *Eucalyptus pellita* on bauxite mining areas (Dias *et al.*, 1994) and *Eucalyptus grandis* in Brazil (Garay *et al.*, 2004) but they were

similar between a 3-yr-old *A. mangium* and 3-yr-old eucalypt plantations and grassland (Schiavo *et al.*, 2009). In a 24-yr-old acacia plantations in South China, exchangeable cation levels were similar among three sites supporting either *A. mangium* or *A. auriculiformis* plantations and an open site (Yang *et al.*, 2009). Low pH in acacia plantation soils may lower CEC because of an increase of variable charge in SOM, clay and oxides (Yamashita *et al.*, 2008).

Table 2.4 Soil exchangeable cations and CEC in plantations of some acacia plantations

Species	Age, site condition and location	Soil layer (cm)	K^+ ($cmol_c\ kg^{-1}$)	Na^+ ($cmol_c\ kg^{-1}$)	Ca^{2+} ($cmol_c\ kg^{-1}$)	Mg^{2+} ($cmol_c\ kg^{-1}$)	ECEC ($cmol_c\ kg^{-1}$)	Reference
Acacia mangium	– 24 yrs, degraded soil, S. China	0 – 20	0.019	0.01	0.019	0.006		(Yang *et al.*, 2009)
	– 8 yrs, planted on *Imperata* grassland in Indonesia	0 – 6					4.7	(Yamashita *et al.*, 2008)
		6 – 21					3.5	
	– 3 yrs, clay extracted area in Brazil	0 – 20	0.15	1.3	3.2	2.1	6.9	(Schiavo *et al.*, 2009)
	– South Kalimantan, Indonesia	N/A	0.16 – 0.51	0.02 – 0.06	0.24 – 3.07	0.65 – 2.57		(Simpson, 1992)
Acacia auriculiformis	– 24 yrs, degraded soil, South China	0 – 20	0.017	0.01	0.019	0.005		(Yang *et al.*, 2009)
	– 4 yrs, sandy soil, Congo	0 – 25	0.01	0.04	0.29	0.1	1.01	(Kasongo *et al.*, 2009)
	– 10 yrs, sandy soil, Congo	0 – 25	0.05	0.01	0.65	0.14	1.16	(Kasongo *et al.*, 2009)
	– 17 yrs, sandy soil, Congo	0 – 25	0.02	0.03	0.68	0.2	1.47	(Kasongo *et al.*, 2009)

5) Soil acidity (pH)

Soil acid production by legumes is associated with higher uptake of cations than anions by N_2-fixing plants (Tang *et al.*, 1997). This excess uptake of cations leads to excretion of H^+ by plant roots, the mechanism by which plants regulate their charge balance (Haynes, 1990), and results in decreasing rhizosphere pH (Tang *et al.*, 1997). The form of N uptake by plants is also related to acid production. When the N form in soils is NH_4^+, the product of N_2 fixation, acidity develops, but when N is present as NO_3^- alkalinity develops (Tang *et al.*, 1997). Legumes can produce 0.2 – 1.6 mol H^+ when fixing 1 mol of N (Raven *et al.*, 1990), whereas they can release from 0 – 1 mol OH^- when 1 mol NO_3^- is taken up and assimilated (Bolan *et al.*, 1991). When testing supply of NO_3^- to eight legume species, H^+ production decreased with NO_3^- supply; N_2 fixation also decreased (Tang *et al.*, 1999). Therefore leaching of NO_3^- and plant release of H^+ ions can also lead to more acidic soil.

Acacia plantations are associated with high level of soil acidity (Yamashita *et al.*, 2008; Kasongo *et al.*, 2009; Schiavo *et al.*, 2009; Yang *et al.*, 2009; Wang *et al.*, 2010a; Sang *et al.*, 2012) (Table 2.5). Soil pH in 8-yr-old *A. mangium* was significantly lower, by 1.0 and 0.5 pH units in the 0 – 5 cm and 25 – 30 cm layers, respectively, than in the original *Imperata* grassland (Yamashita *et al.*, 2008). Similarly, pH in an *A. auriculiformis* plantation in Congo decreased from age 1 to 17 yrs and was significantly lower than in nearby savannah (Kasongo *et al.*, 2009). Soil pH was very low in a 5-yr-old mixed plantation of *A. mangium* and dipterocarp planted on top layer of sandy soil in the Malay peninsula, Thailand, with the values of 4.5 and 3.2, in pH_{H2O} and pH_{KCl} respectively, (Norisada *et al.*, 2005). A reversal of pH decline occurred after conversion of *Acacia* plantation to non-legume cropping systems (Tahir *et al.*, 2009).

Table 2.5 Soil pH in plantations of some acacia species

Species	Site condition and location	Age	Layer (cm)	pH_{H20}	pH_{KCl}	Reference
A. mangium	– Degraded soil, S. China	24	0 – 20	4.13		(Yang *et al.*, 2009)
	– Degraded soil, S. China	23	0 – 10	3.81		(Wang *et al.*, 2010a)
	– Clay extracted area, Brasil	3	0 – 10	5.5 → 5.0		(Schiavo *et al.*, 2009)
	– Planted on *Imperata* grassland in Sumatra, Indonesia	8	0 – 20	4.30	3.80	(Yamashita *et al.*, 2008)
			20 – 40	4.20	3.70	
	– South Sumatra, Indonesia	2-5.5	0 – 20	4.10 – 4.60	3.60 – 3.90	(Nurudin, 2007)
	– South Kalimantan, Indonesia	N/A	0 – 10	3.89		(Simpson, 1992)
A. auriculiformis	– Degraded soil, South China	24	0 – 25	4.97 → 4.72	4.30 → 4.20	(Yang *et al.*, 2009)
	– Degraded soil, South China	23	0 – 20	4.31		(Wang *et al.*, 2010a)
	– Sandy soil, Congo	4	0 – 25	4.97 → 4.72	4.30 → 4.18	(Kasongo *et al.*, 2009)
			25 – 50	4.89 → 4.78	4.27 → 4.18	
		10	0 – 25	4.97 → 4.61	4.30 → 4.18	
			25 – 50	4.89 → 4.65	4.27 → 4.18	
		17	0 – 25	4.97 → 4.51	4.30 → 4.15	
			25 – 50	4.89 → 4.50	4.27 → 4.10	

→ shows the decrease between two measurements

Low soil pH limits N_2-fixation of legumes (Munns and Franco, 1982; Munns, 1986; Schubert *et al.*, 1990; Graham *et al.*, 1994), affects survival and persistence of *Rhizobium*, reduces nodulation and delays nitrogenase activity (Zahran, 1999). This is attributed to the effect of high H^+ ion concentration in the soil on *Rhizobium* (Graham *et al.*, 1994). However, strains of rhizobia have differing tolerance to H^+ (Graham *et al.*, 1994; Zahran, 1999). Graham *et al.* (1994) tested 45 *Rhizobium, Azorhizobium* and *Bradyrhizobium* strains at a range of pH levels. Only some strains grew at pH 4.25, most grew at pH >4.5; fast-growing were less tolerant than slow-growing strains to low pH (Graham *et al.*, 1994). Thus selection of acid-tolerant strains may improve nitrogen fixation.

b) Soil physical properties

1) Soil texture, structure and compaction

The vegetation on a site can affect the development of soil structure and to some degree soil texture, via SOM inputs and humus increase. Vegetation cover also reduces the potential for erosion, so it maintains field texture. Tahir *et al.* (2009) showed that fine sand, clay and silt content increased with tree density in planted *Acacia senegal*; in contrast, coarse sand content was higher in pure annual crops. Higher water and wind erosion associated with annual crops than acacia may explain these differences. Soils under tree-based systems are also less susceptible to erosion as they promote formation of stable aggregates with humic compounds (Tahir *et al.*, 2009).

The levels of topsoil soil compaction as measured by bulk density (BD) have been shown to vary among land-management systems. Bulk density was significantly lower in *A. mangium* and *A. auriculiformis* plantations than at an open site (Yang *et al.*, 2009); it was also lower in systems inter-cropped with *A. senegal* than in pure annual cropping systems (Tahir *et al.*, 2009). Vegetation coverage plays an important role in preventing soil compaction as it facilitates enhancement of SOM, soil organisms and root penetration.

2) Soil water content (SWC)

Soil water content is determined by soil water holding capacity (WHC). Texture, structure, capillarity, porosity and SOM are key elements of soil WHC. Vegetation and SOM inputs affect soil capillary and porosity via differences in the densities of dead roots, the activity of soil macro-fauna, and the formation of organic mineral substances (Bin *et al.*, 2007). Fast-growing acacias can enhance soil WHC through root penetration, increase in SOM and creation of favourable conditions for macro- and micro-organisms. Total soil WHC in the 0 – 40 cm soil layer of four-, seven- and 11-yr-old *A. mangium* plantations were 119, 255 and 357 Mg ha^{-1} respectively; it increased with stand age and was higher than that of an 18-yr *Cunninghamia lanceolata* plantation (Bin *et al.*, 2007). Soils in *A. mangium* plantation had higher WHC than in *A. auriculiformis*, and both were higher than at an open site (Yang *et al.*, 2009). Soil infiltration rate was higher in *A. mangium* than *C. lanceolata* and increased with stand age; this increases was related to decreasing BD and increasing SOM (Bin *et al.*, 2007).

3) Soil temperature

Fast canopy closure of acacia plantations can moderate variation of air and soil temperatures below the canopy (Yang *et al.*, 2009). On hot days, air and soil temperature at 0 – 20 cm depth in 24-yr-old *A. mangium* and *A. auriculiformis* plantations were significantly lower than at an open site (Yang *et al.*, 2009). Diurnal fluctuations in soil temperature at 5 cm depth were less in mixed acacia/dipterocarp plantations than plantation dipterocarp only; on hot days, air and soil temperatures were lower in the mixed planting (Norisada *et al.*, 2005). More equitable below-canopy environments can assist the survival and growth of understorey species and foster soil organism activity.

c) Soil biology

Acacia plantations provide good habitat for soil organisms compared to other species, and perform better recruitment of soil macro- and micro-organisms. The number of bacteria, fungi and phosphate solubilisers was higher in a 3-yr-old *A. mangium* plantation than similar-aged *Eucalyptus* plantation and grassland (Schiavo *et al.*, 2009). *Acacia mangium* also demonstrated better recruitment of soil macro-arthropod communities than *Eucalyptus grandis* (Pellens and Garay, 1999). Total biomass of soil animals in 7- to 9-yr-old *A. auriculiformis* plantations planted on degraded land was 18 g m^{-2}, significantly higher than in nearby barren land (0.33 g m^{-2}) (Peng *et al.*, 2005). A significant correlation between soil organism population and SOC indicates that the large amounts of nutrient-rich litter deposited by acacia facilitate the development of the populations (Pellens and Garay, 1999; Schiavo *et al.*, 2009).

Monocultural plantations can nevertheless lead to a decline of soil organism diversity. A comparison of soil macro-fauna between an *A. mangium* plantation and natural forest showed that although the total biomass of macro-fauna was greater in the plantation, there was a simplification of community structure in many taxonomic groups; species of termites, ants, fly larvae, click beetle larvae and other beetle larvae decreased following vegetation change (Tsukamoto and Sabang, 2005). Tree-species mixtures should lead to greater soil organism diversity.

2.2.1.3. Ecological concern of monoculture exotic acacia

Acacia species belong to one of the three tree taxa (viz *Acacia, Eucalyptus* and *Pinus*) that have large planting areas outside their native ranges (Richardson *et al.*, 2011). At least 386 Australian acacia species have been introduced to other countries and of these, at least 23 are considered invasive (Richardson *et al.*, 2011). Nevertheless perceptions about them differ over time and have become increasingly complex (Richardson *et al.*, 2008; Richardson *et al.*, 2011). While their invasiveness leads to a wide range of negative impacts on ecosystems (Le Maitre *et al.*, 2011; Morris *et al.*, 2011), site history and forest management practices can dictate the outcome (Feyera *et al.*, 2002). Thus invasions do occur where natural forest has been converted into acacia plantations, but where acacia is planted into degraded ecosystems, recovery of favourable conditions can lead to recruitment of native-tree species seedlings (Otsamo, 2000b; Peng *et al.*, 2005). Exotic species in many cases have been reported to bring ecological benefits (Bouillet and Bernhard-Reversat, 2001; Huttel and Loumeto, 2001; Feyera *et al.*, 2002),

particularly where degraded landscapes cannot be restored by native species, or can be restored quickly and effectively by non-natives (Ewel and Putz, 2004; Lugo, 2004).

Tropical acacia plantations facilitate regeneration of local species when established on degraded landscapes. In an *A. auriculiformis* plantation planted on degraded land in South China, brushwood formed seven years after establishment, and a significant number of native-tree species appeared after 21 yrs (Peng *et al.*, 2005). Acacia also performs better recruitment than other species, for example, highest abundance of regenerated native species was found in an *A. mangium* plantation compared with *Gmelina arborea* and *Paraserianthes falcataria* plantations (Otsamo, 2000b). There is thus potential for restoration of degraded landscapes to native species in the tropics, particularly if silvicultural treatments that accelerate this successional process can be developed, such as enrichment planting and management of negative effects among species to facilitate development of the natives (Parrotta *et al.*, 1997).

Species mixtures diminish risk of ecological damage (Kelty, 2006; Nair, 2007; Lamb *et al.*, 2012). Monocultures of acacia increase risk by introducing monocultural and exotic effects, and it is necessary to analyse each separately (Lamb, 2011b). Mixtures are less vulnerable to pests and diseases than monocultures because they reduce host concentration, impairing the ability of the pest and disease to find the host, and creating more diverse habitats to recruit their natural enemies (Watt, 1992). While exotic plantations appear at less risk of pest attack than plantations of indigenous tree species (Nair, 2007), other pests and diseases build up with time, and if accidently introduced, lack of natural local enemies can lead to more severe outbreaks (Lamb, 2011b). Monocultures may recover some functions and natural processes (Lamb, 2011b), but repeated applications of treatments such as clear cutting, intensive soil

preparation, tending and fertilising prejudice environments and habitats for other organisms, causing the loss of local biodiversity, especially where natural ecosystems are converted to plantation (Kelty, 2006). Conversely, mixed-species plantation can provide more diverse habitats and niches for local organisms, which in turn will accelerate recovery of the local ecosystems. Closer-to-nature management practices applied to mixed-species plantations such as selective harvesting and assisted natural regeneration will also enhance ecological benefits from these forests.

Ewel and Putz (2004) stated that "blanket condemnation of alien species in restoration efforts is counterproductive". Therefore, where exotic species do not threaten surrounding ecosystems or can bring better ecological services, they can be used without major concern of ecological damage. This still requires a comprehensive understanding of its biotic and abiotic effects, potential for ecological or economic restoration, impact on stakeholders, potential consequences to the landscape, and effects of any reversion of its use (Ewel and Putz, 2004). "Humans cause invasions, humans perceive invasions, and humans must decide whether, when, where and how to manage invasions" (Richardson *et al.*, 2008).

2.2.2. *Acacia* as nurse crop

2.2.2.1. Nurse crop

From a successional viewpoint, nurse crops can be seen as the pioneers which create the favourable site conditions for establishment of the late-successional species. Based on this principle, the nurse-crop technique fundamentally relies on the theory of facilitation

and competition (Forrester *et al.*, 2006; Ren *et al.*, 2008). According to Franco and Nobel (1989) “Nurse crops facilitate the growth and development of other plant species (target species) beneath their canopies by creating favourable microhabitats for seed germination and/or seedling recruitment”. Facilitation refers to the positive effect of certain plants on establishment and growth of others without harm. This happens when the effect of one species on environment favours the adaptation and growth of another (Bruno *et al.*, 2003). This can be a direct effect by changing site factors such as light, temperature, water or nutrients through shading or nutritional symbioses, or indirect by removing or deterring competitors (Miller, 1994; Callaway and Walker, 1997; Bruno *et al.*, 2003). These effects of nursing have been recognized to act as "successional catalysts" for facilitating restoration of degraded lands (Parrotta *et al.*, 1997), that would otherwise not occur because of environmental constraints (Oberhauser, 1997), especially in disturbed environments (Connell and Slatyer, 1977; Bruno *et al.*, 2003).

2.2.2.2. Nursing effects

The nursing effect can be attributed to the environmental and soil factors that directly affect the establishment and growth of target trees. The two key benefits offered by acacia as a nurse-crop species are shading and enhanced nutrient cycling (Padilla and Pugnaire, 2006). These benefit the establishment of target species as follows:

a) Survival rate after transplanting

Shade-adapted species in particular are protected from transplanting shock and photoinhibition by shade, which enhances their establishment and survival. High

radiation loads can also be associated with high transpiration rates (Pallardy, 2008). When transplanted seedlings are not adapted to their new environments, unless protected by shade, water loss may lead to death of seedlings. Acacia plantations are able to regulate soil moisture content during the planting season(Norisada *et al.*, 2005), and air and soil temperature (Yang *et al.*, 2009) thereby supporting settlement of seedlings; these effects have resulted in significantly higher survival rates at 45 month-old of three dipterocarps: *H. odorata*, *Dipterocarpus alatus* and *Shorea roxburghii* with than without the *A. mangium* nurse crop. In the absence of the nurse crop, survival rates varied among species, suggesting a need for different shading intensities among species. The continuing decrease of survival in the non-shading treatment indicated that photoinhibitory effects can be long term, so retention of nurse crops is needed for extended periods (Norisada *et al.*, 2005).

b) Growth rate

When plants are photoinhibited they assimilate less carbon and produce less biomass (Valladares *et al.*, 2005; Gómez-Aparicio *et al.*, 2006); shade-tolerant species photosynthetic rates are significantly reduced in high light conditions (Kelly *et al.*, 2009). Maximum quantum yield of photosystem II (F_v/F_m) is used to measure levels of photoinhibition (Kitajima and Butler, 1975; Maxwell and Johnson, 2000). In the absence of photoinhibition, F_v/F_m is 0.80 – 0.85 (Björkman and Demmig, 1987); photoinhibition may be occurring if F_v/F_m is <0.8 (Vonshak *et al.*, 1994). The use of *A. mangium* and *A. auriculiformis* as nurse crops for three shade-tolerant species *Castanopsis hystrix*, *Michelia macclurei*, and *Manglietia glauca* in South China

decreased photoinhibition. F_v/F_m of the three target species were significantly greater with than without the nurse crop where F_v/F_m was ~0.70 in the period 09:30 – 14:30 h. These effects contributed to significantly higher growth rates of all three target species in the *A. mangium* and *C. hystrix* and *M. macclurei* in *A. auriculiformis* systems (Yang *et al.*, 2009). *Dipterocarpus alatus* and *H. odorata* had significantly better height and diameter growth in a mixed plot with *A. mangium* than when grown alone; without shading total height of *H. odorata* declined because of dieback which may be the effect of photoinhibition (Norisada *et al.*, 2005).

Interplanting with legumes can enhance soil N, and increase growth of the target species. On eroded pasture in Costa Rica, better growth of *Terminalia amazonia* in a mixed planting with the legume *Inga edulis* than when planted alone was attributed to N enhancement by *I. edulis* (Nichols and Carpenter, 2006). Similarly, interplanting N_2-fixers with *Eucalyptus* led to higher N concentration in the litter, and higher growth rate than in the *Eucalyptus* monocultures (Forrester *et al.*, 2006; Laclau *et al.*, 2008).

c) Stem quality

Light competition promotes apical growth and self-pruning of the understorey trees which results in a long, strait and clear bole, but may reduce overall growth rate. Increasing light penetration by thinning the nurse crop may increase the growth of the target trees, but beyond a certain level of light intensity may compromise stem form. For example, thinning the *P. radiata* nurse crop led to a significant diameter increase of 5-yr-old *A. melanoxylon*, the target species, but led to decreased height increment, loss of apical growth and rapid development of large size branches, all undesirable features

for high quality stems (Medhurst *et al.*, 2003). Pruning may offset loss of stem form, but can also reduce growth rate; in this experiment growth rate declined when 50% of foliage area was removed by pruning and 12 months was required for foliage to recover to pre-pruning levels (Medhurst *et al.*, 2003). These findings are similar to a parallel experiment with *A. melanoxylon* in native forest where *Eucalyptus obliqua* was the nurse crop (Jennings *et al.*, 2003). A good strategy for thinning nurse crops and pruning target trees is needed for optimising growth rate and stem quality.

d) Risk of pests and disease, fire, and invasive weeds

Mixed-species plantations have a lower risk of pests and diseases than monocultures (Watt, 1992). Nurse trees such as *Leucaena* sp. can limit fire damage to target trees by reducing the fuel load (Santiago-García *et al.*, 2008). Both *Acacia* hybrid and *A. auriculiformis* have been reported as being low risk for forest fires, and good species for establishment of green belts for fire-breaks, because of the thickness and high water content of leaves and bark (Thanh, 2008). In Indonesia, 6.5-yr-old *A. mangium* completely eradicated a strong invasion of *Imperata cylindrical*; no observation of regrowth where artificial 192m^2 gaps were created within the plantation (Otsamo, 1998b). The same grass was eradicated by a 4-yr-old *A. mangium* plantation also, but thirteen months after a 260 m^2 gap was created *I. cylindrica* had regrown, though it was only 1.4% total dry biomass of regrowing shrubs and grasses (Otsamo, 2000b).

2.2.2.3. Negative effects of nurse crops

Negative effects can be understood as a negative consequence of the interaction between two or more plants or populations (Vandermeer, 1989). Understanding and managing these negative effects, either allelopathy or completion, is essential when using the nurse-crop planting model.

a) Allelopathy by acacias

Allelopathy is usually related to chemical interactions between species, which may favour or adversely affect other plants (Kruse *et al.*, 2000; Oyun, 2006). Negative effects occur when residues or exudates of one species inhibit the development of another (Gonzalez *et al.*, 1995). *Acacia mangium* decreased the germination rate of the native tree species *Machilus odoratissima, Lithocarpus ducampii* and *Pterocarpus macrocarpus* in Vietnam (Mung *et al.*, 2009). Leachates extracted from leaves, roots and decomposed litter of *A. mangium* were used in germination tests; rates were lowest with leaf leachates. Root leachates only decreased germination rate of *L. ducampii*; decomposed litter leachates did not affect germination (Mung *et al.*, 2009). Similarly, leaf leachates of *A. auriculiformis* significantly decreased germination rate, extended germination time and led to a decline in seedling vigour of *Zea mays*; the effects were directly proportional to concentration of the leachate. Allelopathic effects of non-tropical acacia species on crops have also been reported (Gonzalez *et al.*, 1995; Lorenzo *et al.*, 2008; Noumi and Chaieb, 2010). A general conclusion is that allelopathy is more serious with leachates from leaves, the effects are stronger when decomposition commences, and depend on the soil where decomposition takes place (Gonzalez *et al.*,

1995); there is no effect from decomposed materials (Mung *et al.*, 2009). Allelopathic effects of acacia may mainly be a constraint for natural regeneration as it mostly affects seed germination and radicle growth; seedlings planted under acacia canopies are unlikely to be affected.

b) Competition in a nurse-crop planting model

Competition is a contest between individuals or populations for light, soil water and nutrients. Competition for water and nutrients tends to be symmetrical, because uptake per unit root surface area is similar between large and smaller plants. Competition for light is asymmetrical as taller plants shade smaller plants but not vice versa (Weiner, 1990; Forrester *et al.*, 2006). Although fast canopy closure of acacia plantations is expected to lessen soil evaporation rate, their high rates of photosynthesis and transpiration, low water-use efficiency and high stem moisture content results in high consumption of water (Yamamoto *et al.*, 2003; Inagaki *et al.*, 2008). Cienciala *et al.* (2000) found that daily water consumption in 9-yr-old *A. mangium* was high and associated with high sap flow rates and canopy transpiration. This occurred even under very high evaporative conditions, suggesting low canopy resistance to climatic variables of this species provided there was access to sufficient soil water (Cienciala *et al.*, 2000). *Acacia mangium* can have a substantial night-time sap flow, which can account for 15 – 30 % of the total transpiration (Wang *et al.*, 2011). The moisture contents in the sapwood and heartwood of *A. mangium* and *A.* hybrid were also reported as extremely high, higher than in *A. auriculiformis* and *Eucalyptus deglupta* (Yamamoto *et al.*, 2003). The heartwood of *A. mangium* and *A. hybrid* also had higher moisture content than

sapwood, though this might be caused by heart rot and result from "wet-heartwood". During rain-free days, soil water content at 20 cm depth declined faster in a mixed *A. mangium* and dipterocarp plantation than in a pure dipterocarp plantation, although it was higher during rainy period (Norisada *et al.*, 2005). These suggest that in nurse-cropping systems, competition for water may occur between acacia and the target species during dry season. As competition for nutrients is symmetrical, it may not affect the nutrient supply of the understorey species.

As acacia is fast-growing, the most efficient use of light is likely to be gained when the target species is shade tolerant during establishment. However, managing light competition in this model requires understanding the growth rate, light demand, crown structure and foliar phenology of the target species, all of which are complementary (Kelty, 2006). Light demand may change during development, usually from shade-tolerant to light-demanding, so competitiveness may become more asymmetric with time (Forrester *et al.*, 2006). Timing silvicultural interventions to manage these negative effects is crucial.

2.3. Summary

The review has shown that while shading may support regeneration of *H. odorata* in natural forest, deep shading in plantations suppresses its growth. However, lack of information about the appropriate level of shading for seedling development still exists. While changes to leaf traits and leaf function of *H. odorata* with increasing light levels have been reported, the results are mostly based on natural habitat and shade-house experiment; there is a lack of information on light requirements of this species in nurse-

crop systems, or in degraded environments, and on levels of interspecific competition between *H. odorata* and nurse crops. Eco-physiological characters of plants may change with plant development, so observation for a period of time is necessary. A comprehensive approach based on information from field trials is needed.

Acacia is potential tree for reclaiming degraded landscapes because of the many positive effects it brings to the planting environment. Its fast growth rate and N-fixing ability accelerate nutrient cycling. As a result, the key soil properties and functions can be significantly improved and better than by other fast-growing species. Rapid canopy closure regulates the microclimate so that favourable conditions are present for soil organism activities and the re-establishment of native-plant species and other organisms lost from the ecosystem. Shading increases the survival rate of the target species by avoiding planting shock and photoinhibition. Improved nutrients by nurse crops can lead to better growth rates than without nurse crops. Stem quality and a longer bole of the target trees are promoted by self-pruning. Pest and disease attacks may be reduced. Nurse trees also suppress invasive weeds, and can mitigate damage by forest fires.

However, acacia species differ in the rate at which these values are recaptured and information about how soon these effects occur for each species still needs to be examined. This study uses a relatively new species *A.* hybrid, so information about site improvement by this species is needed to verify its potential benefits. High level of soil pH and water consumption, particularly during the dry season may constrain the target species. Its high vigour means that potential biological invasion may also be a concern. Unsuccessful cases related to using acacia as nurse crops mainly related to poor understanding of the interactions between nurse and target trees; light competition was

the most serious problem. To use acacia as nurse crop, a comprehensive understanding of interactions between the planting species is required.

Acacia hybrid as nurse crops for re-planting *Hopea odorata* in Vinh Cuu district, Dong Nai province. Die-back happened in *H. odorata* at the end of dry season could be due to inter-specific competition for water. Photo: Tran Lam Dong, in May, 2011.

Chapter 3 Site conditions for regeneration of *Hopea Odorata* Roxb. In natural evergreen Dipterocarp forest in Southern Vietnam. Pages 52 – 77

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Chapter 4

IMPACT OF SHORT-ROTATION *ACACIA* HYBRID PLANTATIONS ON SOIL PROPERTIES OF DEGRADED LANDS IN CENTRAL VIETNAM

ABRIDGED TITLE: IMPACT OF *ACACIA* HYBRID ON DEGRADED SOILS

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Abstract

Acacia hybrid (*A. mangium* × *A. auriculiformis*) is the main species planted for short-rotation forestry in Vietnam. In this study, the effect of these plantations on some key properties of degraded gravelly soils in Central Vietnam was assessed. Soil samples were collected from second- or third-rotation plantations representative of five age classes (0.5- to 5-yr-old), and in adjacent abandoned lands as controls. Compared to abandoned land, stock of total soil carbon was significantly higher at ages 0.5, 1.5, 2.5 and 5 yrs (18.4 – 19.5 *v.* 13.0 Mg ha^{-1}), total nitrogen at ages 0.5 and 1.5 yrs (1.5 – 1.7 *v.* 1.0 Mg ha^{-1}), exchangeable calcium at ages 0.5, 1.5 and 2.5 yrs (215 – 294 *v.* 42 Mg ha^{-1}), magnesium at ages 0.5, 1.5, 2.5 and 3.5 yrs (39 – 48 *v.* 19 Mg ha^{-1}), and sodium at all ages (46 – 59 *v.* 5 Mg ha^{-1}). Electrical conductivity was significantly higher at all ages (58.5 – 69.4 *v.* 32.7 µS cm^{-1}). Differences in extractable phosphorus and exchangeable potassium were not significantly different between plantations and abandoned land. Bulk density was significantly lower in plantations than abandoned land at all ages (1.36 – 1.42 *v.* 1.55 Mg ha^{-1}), pH_{CaCl2} at ages 0.5 and 5 yrs (3.78 – 3.84 *v.* 3.98), and pH_{H2O} at age 5 yrs (4.30 *v.* 4.52). Because the soils were gravelly, differences in concentration of total carbon and nutrient between abandoned land and plantations were not the same as those for stocks after correction for gravel content and bulk density. Within a rotation, most soil properties did not change significantly with plantation age, although they appeared to decrease during the first three years; total carbon then recovered to initial levels, but total nitrogen and exchangeable cations remained lower. Some soil properties were strongly related to gravel content and elevation, but not with growth rate. We concluded that consecutive plantings of short-rotation *Acacia* hybrid on degraded and abandoned land can lead to changes in some soil properties.

Keywords

Degraded land, gravelly soil, nutrient stock, soil amelioration, nitrogen fixation

Summary text for non-experts

One-quarter of the area of Vietnam is at risk of soil degradation because of unsustainable logging and land-use practices. Consecutive plantings of short-rotations of plantation *Acacia* can have positive effects on the chemical and physical properties of degraded, strongly acidic gravelly soils with low organic carbon in Central Vietnam, though they remain strongly acidic. As the availability of soil nutrients is related to gravel content, element stock per unit volume provides a better measure of soil element levels than concentration.

4.1. Introduction

Mismanagement of forests in tropical environments has led to large areas of degraded land in several countries (Lamb, 2011b). The loss of forest cover due to widespread herbicide use during the Vietnam war, and unsustainable logging and land-use practices between the 1960s and 1980s (Sunderlin and Ba, 2005), were the major factors resulting in soil degradation in Vietnam (MARD, 2005). Water and wind erosion following loss of tree cover removes topsoil leading to reduced biological activity, poor soil structure and depletion of nutrient capital (Lal *et al.*, 1989; Lal, 1996b). Such changes also result in soil compaction, which in turn accelerates erosion by the feedback process of increased run-off (Lal, 1997). In Vietnam, 9.4M ha of land are at risk with monsoonal rainfalls causing topsoil erosion up to 10 t ha^{-1} yr^{-1}. Soil in run-off can contain 1% total organic carbon (TC), 0.1% total nitrogen (TN), 0.035% extractable phosphorus (Ext-P) and 0.042% exchangeable potassium (Ex-K) (Sam *et al.*, 2006). The losses of these natural capital stocks and soil function take a long time to recover through pedogenesis.

To halt erosion and return degraded areas to productive use, appropriate artificial interventions which are based on the level of degradation and the goal of restoration must be applied (Heneghan *et al.*, 2008). A common approach uses vegetation adapted to degraded soils. While a range of species are used for soil conservation and restoration, tropical acacias are widely planted in South-east Asia and South China (Turnbull *et al.*, 1998; Yang *et al.*, 2009; Wang *et al.*, 2010a). Their tolerance of very poor soil conditions and ability to produce a marketable product in a rotation of < 10 yrs make them a preferred choice (Cole *et al.*, 1996; Turnbull *et al.*, 1998; McNamara *et al.*, 2006). Their high productivity and leguminous properties are assumed to be associated with recovery of soil nutrients and an acceleration of nutrient

cycling in these degraded soils. For example, total carbon, total nitrogen, extractable phosphorus and some exchangeable cations in soils under acacia plantations were significantly increased by acacias and higher than for other planted species (Bernhard-Reversat, 1996; Yamashita *et al.*, 2008; Kasongo *et al.*, 2009; Schiavo *et al.*, 2009; Yang *et al.*, 2009; Wang *et al.*, 2010a; Sang *et al.*, 2012). These outcomes have been linked to the high amounts of litter deposited by acacia plantations which in principle can lead to increased capacity of the soil to store and supply nutrients and improved site condition. Their fast canopy closure can protect soil from heavy rainfall and create buffered microclimates which facilitate soil biological processes (Binkley and Giardina, 1997; Norisada *et al.*, 2005; Tsukamoto and Sabang, 2005; Schiavo *et al.*, 2009). However, these findings have been associated with long rotations of between 8 to 25 yrs.

In Thua Thien Hue province in Central Vietnam where this study was done, large areas had become extensively deforested and the landscape seriously degraded by the 1980s; the vegetation then became dominated by *Imperata* grasslands and scrub species (McNamara *et al.*, 2006). Since then, the Vietnamese Government and international aid organisations have funded countrywide restoration programs, primarily by introducing exotics including *Eucalyptus* and *Acacia* species (Binh *et al.*, 2004). *Acacia* hybrid, a naturally occurring hybrid of *A. mangium* × *A. auriculiformis*, has become the dominant species for commercial planting since the late 1990s due to its fast early growth, wide adaptation to degraded soils and available product markets, particularly pulpwood in a prevailing cutting rotation of about five years (Kha, 2001; Bueren, 2004; Amat *et al.*, 2010) leading to a mean annual increment (MAI) of between 22 m^3 and 30 m^3 ha^{-1} yr^{-1} (Bueren, 2004; Kha *et al.*, 2006). As a result of these reforestation programs in Thua Thien Hue province, in 2009 there were 14,884 ha *A.* hybrid, 7,692 ha of *A. mangium, A. auriculiformis* and *A. crassicarpa*; and 11,658 ha of

mixtures of *Acacia* and native or *Pinus* species (Forestry Sub-department, Thua Thien Hue province; unpublished data).

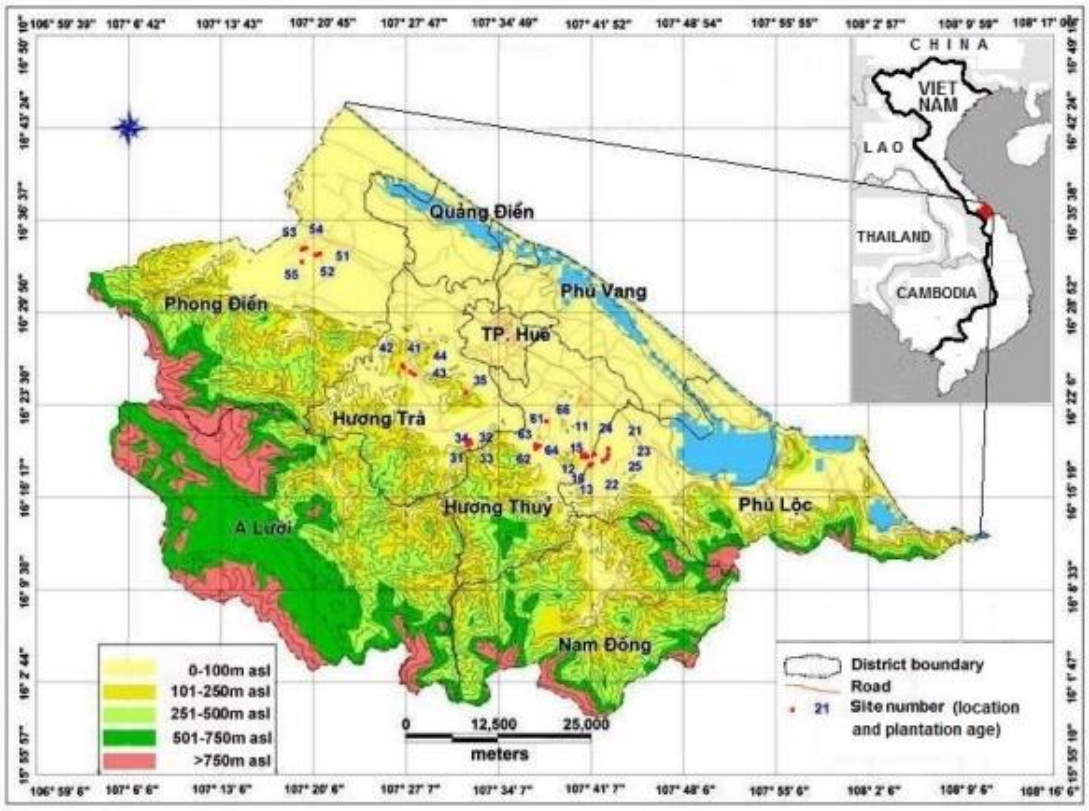
In this paper, we test the hypothesis that consecutive plantings of short-rotation *Acacia* hybrid on degraded land will lead to a cumulative change in some soil properties. This hypothesis is tested by comparing soil properties after one to two short rotations established on degraded lands with those found in adjacent areas having the same land-use history but not planted and abandoned for at least 15 yrs. The change of these soil properties in a single rotation is also examined by testing their dependency on age of these same *Acacia* hybrid plantations. As the soils are gravelly, element stock was calculated by correcting for gravel content. The implications of differences between stock and concentration in carbon and nutrient accounting are discussed.

4.2. Materials and methods

4.2.1. Location, climate and soil

The study sites were located in the hilly lowland areas of Thua Thien Hue province in Central Vietnam at latitude 16.5°N (Fig. 4.1a). The climate is monsoonal with extremely distinct rainy and dry seasons. The average annual rainfall is over 3500 mm, concentrated between September and December, and associated with high frequency tropical typhoons (Fig. 4.1b). Mean annual temperature is 24.9°C; lowest and highest mean monthly temperatures are in January (19.4°C) and June (29.3°C), respectively; mean air humidity is 86.8% (Fig. 4.1b) (Thua Thien Hue Statictical Office, 2010). The main soils are siliceous and sandy, and are classified as Acrisols (Sang *et al.*, 2012), with high proportions (ca. 25%) of weathered coarse fragments (>2 mm) derived from siliceous and parent rocks such as granite, sandstone and gritstone (Que *et al.*, 2010).

a)



b)

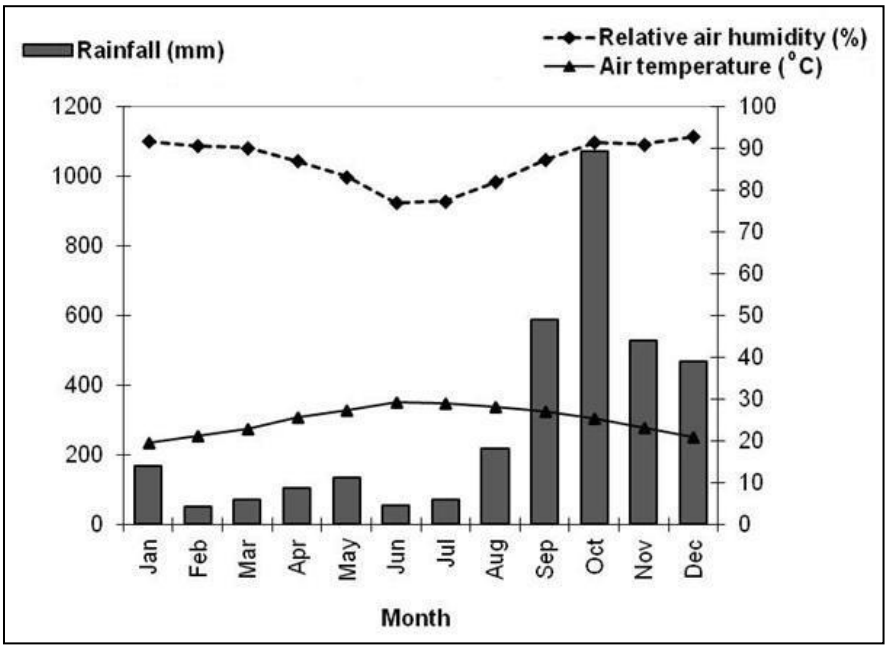


Figure 4.1 (a) Map of the sampled plantations; the first number of each figure (1-6) refers to the location (see Table 4.2) and the second number (1-5) to the age class (0.5, 1.5, 2.5, 3.5 and 5 yrs); and (b) mean monthly rainfall, relative humidity and air temperature from 2005-2009 at Hue City (Thua Thien Hue Statictical Office, 2010)

4.2.2. Site selection

Thirty forested sites in six locations were selected from second- or third-rotation *Acacia* hybrid plantations re-established between 2006 and 2010. They were of five age classes: 0.5, 1.5, 2.5, 3.5 and 4.5-5.5 yr old (hereafter referred to as 5-yr-old) and each age class was represented at the six locations (Fig. 4.1a). This estate was part of a World-Bank supported forest-sector development project (FSDP-WB3) (The World Bank, 2013) and used uniform seedling stock and silvicultural practices (Table 4.1).

Table 4.1 Silviculture applied to the plantations of *A.* hybrid used in this study in Thua Thien Hue, Vietnam

Yr	Month	Activities	Fertiliser
1	Mar – Aug	- Harvesting previous rotation;	
	Jul – Aug	- Burn litter and slash from previous rotation;	
	Aug – Sep	- Dig 40 × 40 × 40 cm planting holes manually or by excavator at 3 × 2 m or 2 × 2 m spacing (1660 to 2500 trees ha^{-1}, respectively);	
	Oct – Dec	- Mix soil in hole with 0.05 kg 16:16:8 N:P:K fertiliser; - Plant clonal cuttings	13.3 kg N + 5.8 kg P + 5.5 kg K ha^{-1}
2	Mar – May	- Weeding and pruning; - Hoe-up topsoil around each seedling and incorporate 0.1 kg 16:16:8 N:P:K in ring between 0.7 – 1.0 m diameter from stem	26.6 kg N + 11.6 kg P + 11.0 kg K ha^{-1}
3	Apr – Jun	- Weeding	
5-6	Mar – Aug	- Harvesting and next rotation	

At each location, one adjacent abandoned site was selected for collecting comparative samples. These sites had the same land-use history as the forested sites in that they had been afforested with either eucalypt, pine or acacia plantations for a brief period prior to 1995, but had then been harvested and abandoned as they were under national high voltage powerlines constructed at that time (hereafter referred to as abandoned land). Plantations were not allowed under the powerlines and the distance between the pylons was around 500 m. The areas selected for sampling showed no sign of disturbance caused by construction. The common indicator for these areas was the dominance of sparse *Rhodomyrtus tomentosa* and *Melastoma candidum*, scrub species which are also indicators of degraded and acidic lands.

4.2.3. Sampling and sample analyses

Sampling was carried out in the dry season from May to August 2010. In each plantation, three to five square 15 × 15 m (225 m^2) sampling plots, depending on the size of the plantation (2 – 3 ha: 3 plots; 4 – 5 ha: 4 plots; and > 5 ha: 5 plots), were used for soil sampling and measurements of tree growth. For plot selection, a transect was first drawn randomly through the longer dimension of the plantation and plots located 30 m from plantation border at each end of the transect. The other plots were evenly spaced between these two end plots. In each plot, a composite mineral soil sample was aggregated from five soil cores randomly collected by a 100-mm diameter auger from 0 – 20 cm depth. The sampling points were located in the centre of the inter-row area to maximise the distance from trees and stumps from the previous rotations located in the same rows, and any disturbance caused by silvicultural operations associated with pit planting. The litter layer was carefully removed before sampling. In addition, three

cores to 20-cm depth were also randomly collected from the inter-row area in each plot for bulk density (BD) analysis using a 53-mm diameter ring. Planting stock, diameter at breast height (DBH), total height, crown length and crown diameter of all trees were measured in each forested plot.

In each of six abandoned-land sites, a plot area similar to that used in the plantations (15 × 15 m) was selected for sampling. Each site met the following criteria: there was no sign of disturbance in the past and the area was at least 100 × 100 m; the plot was located in the middle of that area. A composite sample and three BD cores were collected as controls using the same methods as for plantations.

Geographic location and elevation of each sampling plot were determined by GPS (Garmin 60CSx). The mean of three randomly selected measures of percentage change in elevation per horizontal distance using a straight pole of 4-m length attached to a levelling tool was used to determine the slope of the plot.

Bulk density was determined after the cores were dried at 105^{o}C to constant weight. Gravel (>2 mm) in each BD core was separated using a 2-mm sieve and weighed. Preparation and analysis of the composite soil samples followed the Australian Laboratory Handbook of Soil and Water Chemical Methods (Rayment and Higginson, 1992). The samples were first air-dried and put through a 2 mm sieve. Soil pH_{H2O} and electrical conductivity (EC) were measured by a handheld Lab Navigator (Forston Labs) in a 1:5 mixture of soil and distilled water. Soil pH_{CaCl2} was measured in a 1:5 mixture of soil and 0.01M calcium chloride. Total carbon (TC) and total nitrogen (TN) were determined using a CHNS/O Element Analyser (PerkinElmer). Extractable phosphorus (Ext-P) was determined using the Olsen manual colour method and measured by a spectrophotometer (UNICO 1100RS) at a wavelength of 882 nm.

Exchangeable cations (Ex-K, Ex-Ca, Ex-Mg and Ex-Na) were extracted with 0.01M silver-thiourea $(AgTU)^+$; exchangeable K^+ and Na^+ were determined by flame photometry (JENWAY) and Ca^{2+} and Mg^{2+} by atomic absorption spectroscopy (GBC Avanta). Particle sizes were determined on sub-samples dispersed by heating in water followed by 16 h end-over-end shaking in the presence of NaOH and Calgon. Fractions were determined by settling with a Bouyoucos hydrometer. All data are reported as unit per oven dried weight.

4.2.4. Calculations

Carbon and nutrient stock per hectare were calculated as the product of their concentration in soil fractions <2 mm with bulk density of the fine fraction <2 mm ($BD_{<2mm}$) and the thickness of the soil layer (20 cm), in which:

$$BD_{<2mm} = \frac{W_t - W_g}{V_c}$$

where W_t is total weight of BD core (g); W_g is weight of gravel >2 mm in BD core (g); and V_c is volume of BD core (cm^3)

Basal area (m^2 ha^{-1}) was calculated as the sum of the cross-sectional area over bark at breast height of all individual trees per hectare. Standing volume (m^3 ha^{-1}) was the sum of the standing volume of all individuals per hectare, in which tree standing volume was a product of basal area with tree height and stem form factor (*f*) = 0.495 (Binh, 2003).

4.2.5. Statistical analysis

Differences in soil properties between plantations and abandoned lands were examined by analysis of variance using the PROC GLM procedure in SAS version 9.2. Dunnett's procedure was used to adjust the two-sided P-values to compare the age classes to the abandoned lands (Dunnett, 1955). The dependencies of soil properties and stock of elements on plantation age were modelled after adjustment for effects of gravel content, clay content, slope angle and elevation by a regression approach using PROC MIXED procedure in SAS version 9.2. A random effect corresponding to site was assumed. To ensure that the assumption of homogeneity was met, the analyses were weighted by the reciprocal variances per site. Simple linear regression in IBM SPSS Statistics 21 was used to test the relationship between clay contents and TC and TN of individual plots of all ages, and also between growth of individual plots and soil properties, but only for plots aged 2.5 to 5 yrs.

4.3. Results

4.3.1. Site

The mean altitude of the sampling sites at each location ranged from 24 – 61 m and the mean slope from 11.5 – 23.5% (Table 4.2). The dominant particle fraction <2 mm at all sites was sand which ranged from 60 – 82%, while silt and clay ranged from 4 – 19% and 14 – 22%, respectively (Table 4.2). The gravel content >2 mm was low at location 4 (6% by mass) but otherwise in the range 26 – 48% of the total soil mass (Table 4.2). According to the Australian Soil and Land Survey Handbook (McDonald *et al*. 1998), all locations fell within the same classes for elevation, slope and gravel content, except for location 4 which was in a lower gravel-content class.

4.3.2. Soil properties – effects of consecutive short-rotation plantations

Compared to abandoned land, the stock of total carbon (TC) was significantly higher in plantations at ages 0.5, 1.5, 2.5 and 5 yrs (21.8, 20.7, 18.4 and 19.5 *v.* 13.0 Mg ha^{-1}, respectively), and total nitrogen (TN) at ages 0.5 and 1.5 yrs (1.68 and 1.54 *v.* 1.04 Mg ha^{-1}). The C:N (= TC:TN) ratio was significantly higher in plantations at ages 2.5 and 5 yrs. Although all absolute cation stocks were very low, there were large and significant differences in Ex-Ca, Ex-Mg and Ex-Na which were, respectively, approximately 5×, 2× and 10× higher in the plantations than abandoned land, but there were no significant differences in Ext-P and Ex-K (Table 4.3, Fig. 4.2).

While pH_{CaCl2} was significantly lower by about 0.1 – 0.2 unit in plantations at ages 0.5 and 5 yrs compared to abandoned land, pH_{H2O} was significantly lower only in plantations at age 5 yrs (Table 4.3). In all age classes, electrical conductivity in plantations was significantly higher and BD was significantly lower than those in abandoned land (Table 4.3). There were no significant differences in per cent clay, silt or sand contents, or per cent of gravel to total soil mass (Table 4.3).

The content of gravel >2 mm in the 0 – 20 cm topsoil layer ranged from 30 to 42% of total soil mass among plantation age-classes and was 47% in the abandoned land (Table 4.3). Because of this high gravel content, concentration exhibited a different pattern with plantation age to that for stock. Compared to abandoned land, concentration of TC was only significantly higher in soils of 5-yr-old plantations, and there were no significant differences in TN (Fig. 4.2). While statistical differences in the other element concentrations remained similar to those of stocks, Ex-Ca and Ex-Mg concentration were significantly higher at all ages of plantations (Fig. 4.2).

Table 4.2 Means and standard deviations of site and soil factors at each location in Thua Thien Hue, Vietnam

Factor	Location[#]					
	1	2	3	4	5	6
Altitude (m)	35.3 ± 2.1	26.6 ± 4.5	64.9 ± 18.4	60.7 ± 20.4	24.6 ± 7.3	31.3 ± 13.2
Slope (%)	14.9 ± 3.5	11.5 ± 6.3	23.5 ± 6.2	14.2 ± 4.5	13.7 ± 8.6	17.6 ± 9.5
Clay (% of fraction < 2 mm)	17.5 ± 4.1	14.4 ± 5.8	21.9 ± 4.7	15.9 ± 3.7	18.7 ± 3.9	21.4 ± 3.8
Silt (% of fraction < 2 mm)	9.4 ± 2.7	3.9 ± 2.7	7.0 ± 2.6	5.9 ± 2.4	9.7 ± 3.7	18.7 ± 5.6
Sand (% of fraction < 2 mm)	73.1 ± 5.3	81.7 ± 8.1	71.1 ± 6.3	78.2 ± 5.3	71.6 ± 6.4	59.9 ± 8.7
Gravel > 2 mm (% of total soil mass)	44.1 ± 19.4	26.0 ± 23.9	36.0 ± 11.4	5.8 ± 5.3	47.6 ± 10.2	45.0 ± 14.9

[#] Number of sites at each location was six, i.e. five plantation age classes and one control (abandoned land)

Table 4.3 Means, standard errors and significant differences[#] of soil properties in 0 – 20 cm topsoil of second- or third-rotation *Acacia* hybrid plantations and nearby abandoned lands in Thua Thien Hue, Vietnam

Properties	Abandoned lands	Age of *Acacia* hybrid plantations (yr)				
		0.5	1.5	2.5	3.5	5
TC (Mg ha^{-1})	12.99 ± 1.75	21.76 ± 0.72 *	20.72 ± 0.97 *	18.44 ± 1.06 *	17.64 ± 1.14	19.48 ± 1.34 *
TN (Mg ha^{-1})	1.04 ± 0.08	1.68 ± 0.07 *	1.54 ± 0.08 *	1.29 ± 0.07	1.28 ± 0.09	1.31 ± 0.08
C:N ratio	12.3 ± 0.8	13.1 ± 0.4	13.7 ± 0.4	14.5 ± 0.5 *	14.0 ± 0.5	14.8 ± 0.3 *
Ext-P (Mg ha^{-1})	4.21 ± 1.29	4.56 ± 0.46	3.24 ± 0.28	3.75 ± 0.70	3.54 ± 0.45	3.23 ± 0.55
Ex-K (Mg ha^{-1})	14.81 ± 3.49	17.25 ± 2.75	14.39 ± 1.95	11.93 ± 1.23	11.89 ± 1.60	10.49 ± 0.97
Ex-Ca (Mg ha^{-1})	41.5 ± 4.6	293.6 ± 50.7 **	248.0 ± 29.4 *	214.5 ± 35.2 *	190.7 ± 31.7	182.5 ± 28.2
Ex-Mg (Mg ha^{-1})	19.48 ± 3.76	48.40 ± 6.42 **	40.70 ± 3.78 *	40.14 ± 3.89 *	38.91 ± 3.61 *	34.34 ± 2.24
Ex-Na (Mg ha^{-1})	5.32 ± 1.62	58.49 ± 4.69 **	59.06 ± 7.15 **	58.05 ± 5.55 **	52.65 ± 7.27 **	46.23 ± 6.99 *
pH_{CaCl2} (1:5)	3.98 ± 0.04	3.84 ± 0.04 *	3.86 ± 0.03	3.87 ± 0.03	3.85 ± 0.02	3.78 ± 0.02 **
pH_{H2O} (1:5)	4.52 ± 0.05	4.35 ± 0.05	4.40 ± 0.03	4.43 ± 0.04	4.40 ± 0.04	4.30 ± 0.03 *
EC (1:5) (µS cm^{-1})	32.7 ± 2.2	69.4 ± 5.4 **	60.5 ± 3.6 **	58.5 ± 3.2 **	60.5 ± 3.9 **	69.4 ± 4.3 **
BD (g cm^{-3})	1.55 ± 0.04	1.37 ± 0.02 **	1.42 ± 0.02 **	1.37 ± 0.02 **	1.38 ± 0.03 **	1.36 ± 0.02 **
Clay (% of fraction <2 mm)	19.1 ± 2.0	17.3 ± 0.8	19.6 ± 1.1	16.8 ± 1.4	18.6 ± 1.4	19.2 ± 1.2
Sand (% of fraction <2 mm)	71.0 ± 4.0	74.1 ± 1.9	71.9 ± 1.4	74.9 ± 2.6	71.5 ± 2.9	70.2 ± 2.1
Gravel >2 mm (% of total soil mass)	46.7 ± 10.0	30.2 ± 4.5	32.3 ± 3.7	33.4 ± 4.7	37.6 ± 4.5	42.2 ± 4.3

[#]TC, Total Carbon; TN, total nitrogen; Ext-P, extractable phosphorus; Ex-K, Ex-Ca, Ex-Mg, Ex-Na: exchangeable potassium, calcium, magnesium, sodium; EC, electrical conductivity; BD, bulk density. Significant differences for each plantation age compared with abandoned lands: *$P < 0.05$,**$P < 0.01$; *P*-values are adjusted using Dunnett's procedure for comparison with the abandoned land

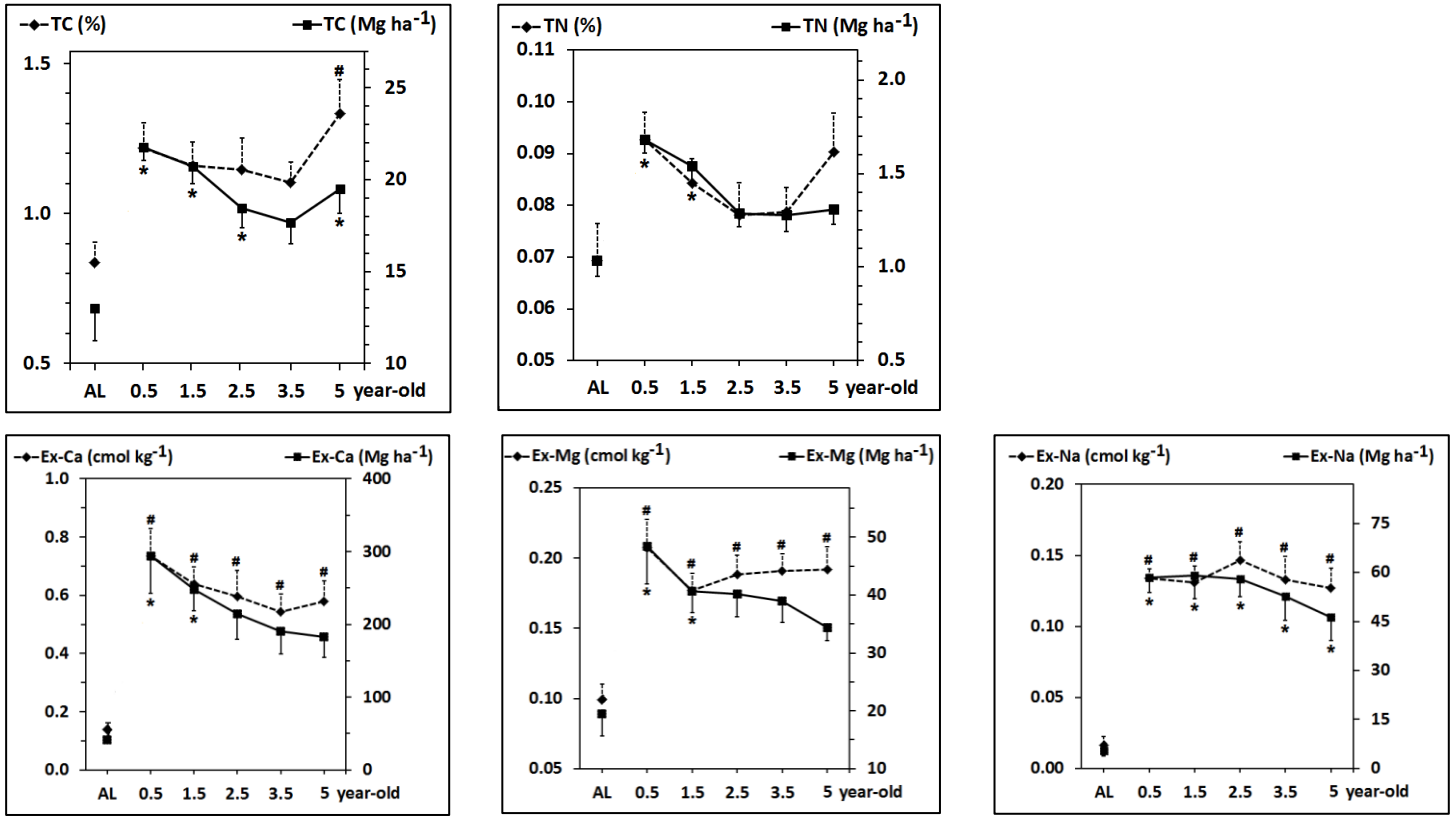


Figure 4.2 Means and one-sided standard error bars of soil carbon and nutrient properties (concentration and stock) in 0 – 20 cm topsoil of 0.5-, 1.5-, 2.5-, 3.5- and 5-yr-old second- or third-rotation *Acacia* hybrid plantations and nearby abandoned lands (AL) in Thua Thien Hue, Vietnam. Element stock per hectare was the product of nutrient concentration with bulk density after correction for gravel content. # and * indicate, respectively, significant difference of element concentration (% TN and TC, and cmol cations kg^{-1}) and element stock (Mg ha^{-1}) between plantation age and AL

4.3.3. Effects of site and rotation age

For nutrient concentration, only the C:N ratio increased significantly with age; concentrations of TC, TN and exchangeable cations did not change significantly (Table 4.4). Although non-significant, the levels of TC and TN appeared to follow an observed trend which indicated a decline until age 2.5 – 3.5 yrs and then an increase at age 5 yrs (Fig. 4.2). Phosphorus and the exchangeable cations also appeared to decline with age (data not shown); EC decreased until age 2.5 yrs but had returned to the initial level at age 5 yrs (Table 4.3).

For nutrient stock, TN (kg ha^{-1}) changed significantly with plantation age; changes for other nutrients were not significant (Table 4.4). The decline with age noted for concentration was greater for nutrient stock and any later-age recovery was either delayed or absent (Fig. 4.2).

Clay content was significantly related to concentration of Ext-P, gravel content to TC and TN, slope to pH_{CaCl2} and altitude to C/N, exchangeable cations (except Ex-Na), pH pH_{CaCl2}, pH_{H2O} and EC (Table 4.4). Similarly, clay was significantly related to stock of Ext-P and altitude to all exchangeable cations (Table 4.4). Examination of the relationships between TC or TN and clay content show that both were significantly related at age 0.5 yr (P=0.009 and <0.001; r^2=0.34 and 0.56, respectively) and at age 2.5 yrs and older (P=0.009 – 0.048 and r^2=0.24 – 0.31 between clay and TC, and P=0.001 – 0.017 and r^2=0.32 – 0.44 between clay and TN). There was no relationship at age 1.5 yrs for both TC and TN (P=0.86 and 0.69; r^2=0.001 and 0.008, respectively).

Table 4.4 Models of soil element concentration or soil nutrient stocks and some key properties of second- or third-rotation *Acacia* hybrid plantations in Thua Thien Hue, Vietnam

Independent variable	Effect	Dependent variable										
		TC[#] (%)	TN	C/N	Ext-P (mg kg^{-1})	Ex-K	Ex-Ca (cmol kg^{-1})	Ex-Mg	Ex-Na	pH_{CaCl2}	pH_{H2O}	EC (µS cm^{-1})
	Intercept	0.975	0.078	15.19	2.758	0.007	0.41	0.112	0.133	3.794	4.268	35.78
Clay (%)	Estimate				–0.037							
	P	n.s.	n.s.	n.s.	0.032	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Gravel content	Estimate	0.47	0.029									
(% of BD)	*P*	0.001	0.016	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Slope (°)	Estimate									–0.009		
	P	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.027	n.s.	n.s.
Altitude (m)	Estimate			–0.049		0.0003	0.006	0.002		0.004	0.003	0.639
	P	n.s.	n.s.	<0.001	n.s.	<0.001	0.011	<0.001	n.s.	0.005	0.047	<0.001
Age	Estimate			0.319								
	P	n.s.	n.s.	0.021	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
		(Mg ha^{-1})			(kg ha^{-1})		(kg ha^{-1})					
	Intercept	21.47	1.325		5.262	6.0839	132.27	26.8626	53.2934			
Clay (%)	Estimate				–0.07							
	P	n.s.	n.s.		0.01	n.s.	n.s.	n.s.	n.s.			
Slope (°)	Estimate											
	P	n.s.	n.s.		n.s.	n.s.	n.s.	n.s.	n.s.			
Altitude (m)	Estimate		0.008			0.2829	2.939	0.5461	0.4329			
	P	n.s.	<0.001		n.s.	<0.001	0.004	<0.001	0.0227			
Age	Estimate		–0.089									
	P	n.s.	0.0032		n.s.	n.s.	n.s.	n.s.	n.s.			

[#] TC, Total Carbon; TN, total nitrogen; Ext-P, extractable phosphorus; Ex-K, Ex-Ca, Ex-Mg, Ex-Na: exchangeable potassium, calcium, magnesium, sodium; EC, electrical conductivity. Shown are the model coefficients and their significant *P* values ($P < 0.05$). n.s., not significant ($P \geq 0.05$)

Table 4.5 Means and standard deviations of tree density, diameter at breast height, total height, basal area, standing volume and mean annual increment of 0.5-, 1.5-, 2.5-, 3.5- and 5-yr-old second- or third-rotation *Acacia* hybrid plantations in Thua Thien Hue, Vietnam

Stand description	Age of *Acacia* hybrid plantations (yr)				
	0.5	1.5	2.5	3.5	5
Density (tree ha^{-1})	2015 ± 215	2036 ± 433	2137 ± 495	1846 ± 331	1456 ± 542
DBH[#] (cm)	0.54 ± 0.31	4.40 ± 0.85	7.56 ± 0.89	9.23 ± 0.69	11.86 ± 1.36
Height (m)	1.62 ± 0.41	5.39 ± 0.97	8.71 ± 0.64	11.55 ± 1.46	15.41 ± 1.31
Crown diameter (m)	1.12 ± 0.29	2.27 ± 0.41	2.57 ± 0.33	2.75 ± 0.29	3.19 ± 0.54
Basal area (m^2 ha^{-1})		3.59 ± 1.37	10.58 ± 2.40	13.85 ± 3.30	17.40 ± 3.41
Standing volume (m^3 ha^{-1})		10.5 ± 5.2	47.7 ± 12.7	84.5 ± 26.6	139.3 ± 34.5
MAI (m^3 ha^{-1} yr^{-1})		7.0 ± 3.5	19.1 ± 5.1	24.1 ± 7.6	28.7 ± 5.9

[#] DBH – diameter at breast height, MAI – mean annual increment.

4.3.4. Relationship between tree growth and soil properties

All measured variables indicated that growth rates were relatively high throughout the rotation; mean MAI of 5-yr-old plantations was 28.7±5.9 m^3 ha^{-1} yr^{-1} (Table 4.5). There were weak, though still significantly positive linear relationships between both pH_{CaCl2} (r^2=0.14; *P*=0.003) and pH_{H2O} (r^2 = 0.10; *P*=0.012) and mean annual DBH increment, between elevation and mean annual DBH increment (r^2=0.09; *P*=0.016), and between elevation and mean annual height increment (r^2=0.16; *P*=0.001). A negative linear relationship was found between C:N ratio and mean annual DBH increment (r^2=0.12; *P*=0.005). There were no relationship between other soil properties and tree growth.

4.4. Discussion

This study has shown that soils after planting with one to two short rotations of *Acacia* hybrid when compared to soils in abandoned land are associated with increases in soil carbon, though these are more apparent in stock than concentration. There were also significant increases in stock of TN but not in concentration of TN, Ext-P or Ex-K. While significantly higher Ex-Ca, Ex-Mg, Ex-Na and sustained increases in electrical conductivity were generally observed, these were accompanied by slightly lower pH in some age classes. Within the measured rotations, age had very little effect on the soil variables measured, though clay, gravel content and altitude did. The soils used in this study were degraded, strongly acidic, leached, and low in TC, so the absolute changes in soil nutrients and TC were small. Nevertheless, MAIs approached 30 m^3 ha^{-1} yr^{-1} at age five years showing that *Acacia* hybrid can be an economic crop on soils with meagre nutrient levels. These results are now discussed in the context of the changes of

soil properties between soils planted with one to two short rotations of *Acacia* hybrid and those of abandoned land, soil change within a single rotation, and the importance of considering nutrient stock in such an analysis.

4.4.1. Soil properties change after one to two short rotations

Vegetation cover is crucial to the recovery of soil organic matter (SOM) on degraded sites, and SOM is the reservoir of soil fertility (Craswell and Lefroy, 2001). In *A. mangium* plantations, there is a significant relationship between biomass production and TC in soil (Sang *et al.*, 2012). In this study, the stock of TC at age 0.5, 1.5, 2.5 and 5 yrs in second- and third-rotation *Acacia* hybrid plantations became significantly higher than in adjacent abandoned-land sites which had only supported scrub vegetation for the previous 15 yrs (21.8, 20.7, 18.4 and 19.5 *v.* 13.0 Mg ha^{-1}, respectively). A significant difference may have emerged in the earlier rotation if the current conventional land preparation practice in Thua-Thien-Hue province of burning the accumulated litter and slash from the previous rotation had been avoided (Table 4.1). Previous studies have also shown that TC (%) in longer rotations of *A. mangium* and *A. auriculiformis* planted on degraded soils is significantly higher than in adjacent scrublands and grasslands (Kasongo *et al.*, 2009; Yang *et al.*, 2009; Wang *et al.*, 2010a). Thus tropical *Acacia* species appear to have the ability to contribute to the recovery of SOM. These tropical acacias are very fast growing and quickly provide high litter deposition rates of between 9.4 to 11.1 t ha^{-1} yr^{-1} in *A. mangium* (Li *et al.*, 2000; Hardiyanto and Wicaksono, 2008) and 4.8 to 6.7 t ha^{-1} yr^{-1} in *A. auriculiformis* (Li *et al.*, 2000; Huong *et al.*, 2008) plantations. *Acacia* hybrid, the natural hybrid between these species, is reported to have

higher growth rates than its parents (Kha, 2001; Bueren, 2004), so even higher rates of litter production are expected.

Total nitrogen stock (TN) was significantly higher in only the first and second year of the rotation (1.68 and 1.54 Mg ha^{-1} *v.* 1.04 Mg ha^{-1}) when compared with abandoned land. Acacias fix atmospheric N and deposition rates of tropical *Acacia* species can exceed 100 kg N ha^{-1} yr^{-1} (Bernhard-Reversat, 1996; Galiana *et al.*, 2002; Yang *et al.*, 2009). This N is mainly released through the litter and root exudates (Brockwell *et al.*, 2005; Forrester *et al.*, 2006). As tropical acacias have relatively low decomposition rates compared to some other fast growing species (Li *et al.*, 2001), and low N mineralisation and nitrification rates (Wang *et al.*, 2010b), N can remain trapped in the litter fraction for longer periods. This may be associated with the significant increase in the soil C:N ratio during the rotation in this study. Burning of accumulated litter during land preparation (Table 4.1) resulting in losses of sources of N, and large amounts of N uptake by *Acacia* hybrid associated with its high rate of growth, may be other reasons for the low TN concentration in soils. Where tropical acacias have been managed over longer rotations, TN was found to be significantly higher than in adjacent scrub- and grass-lands (Macedo *et al.*, 2008; Kasongo *et al.*, 2009; Yang *et al.*, 2009).

Phosphorus is often the most limiting nutrient for the growth of legumes (Munns and Franco, 1982) and in natural systems P is replenished from mineral weathering (Walker and Syers, 1976). Little or no enhancement of Ext-P stock in the topsoil layer is therefore expected and after 5 yrs of short-rotation *Acacia* hybrid forestry in this study, Ext-P was not significantly different from that in the abandoned lands. There is an accepted belief that legumes have a high demand for P for their nitrogen fixation, hence the high P concentration in their nodules (Sun *et al.*, 1992a; Sprent, 1999). At the sites

used here in Central Vietnam, the soils were highly siliceous and coarse textured with low natural P levels. The primary source of P for the trees was probably from the fertiliser applied early in the rotation; P may also have been depleted in harvested products. Longer rotations may be necessary for recovery of Ext-P levels (Yang *et al.*, 2009; Wang *et al.*, 2010a) via plant uptake from deeper less weathered soil layers followed by litter decomposition at the surface.

The low vegetation coverage of the abandoned lands and the sandy soil in this very high and intense rainfall environment in Central Vietnam are probably the major factors contributing to the loss of exchangeable cations by erosion and leaching, and this may be the explanation of the significantly higher stock and concentrations of Ex-Ca, Ex-Mg and Ex-Na in planted *Acacia* hybrid. In addition, clay content and SOM together provide the capacity for retaining exchangeable cations (Astera, 2010). As the clay content was similar between abandoned lands and plantations, the higher TC of plantations may have contributed to the higher concentrations of exchangeable cations. This may also in part be related to cations being added to the soil by burning litter and debris when preparing land for planting. Similar enhancement has also been reported for Ex-Ca and Ex-Mg in a longer rotation *A. auriculiformis* plantation on acidic sandy soil in the Congo (Kasongo *et al.*, 2009), and for Ex-Ca and Ex-Na in longer rotation *A. mangium* and *A. auriculiformis* plantations on degraded soils in South China (Wang *et al.*, 2010a). The stock of Ex-K was not significantly different between plantations and abandoned lands, but the values were extremely low in both treatments, 10.5 – 17.3 *v.* 14.8 Mg ha^{-1}. Ex-K is easily leached in sandy soil (Kasongo *et al.*, 2009) and absorbed by plants in larger amounts than other cations (Verheye, 2006).

In this study, the plantations had been fertilised at planting and in the second year with a total of about 40 kg N ha^{-1}, 17 kg P ha^{-1} and 17 kg K ha^{-1} (Table 4.1). However, wood harvesting and burning associated with previous rotations may have removed a higher amount of nutrients from the sites. Similarly managed *A. mangium* plantations in Indonesia lost 264 – 371 kg N ha^{-1}, 8 – 12 kg P ha^{-1} and 73 – 91 kg K ha^{-1} through harvested stems (Hardiyanto and Wicaksono, 2008). Thus recovery of soil nutrients under acacia plantations is potentially higher.

Although reductions of pH were not always significant, there was some indication that *Acacia* hybrid plantations had approximately 0.1 – 0.2 lower pH_{CaCl2} and pH_{H2O} (3.78 – 3.87 *v.* 3.98 and 4.30 – 4.43 *v.* 4.52, respectively). Nitrogen-fixing plants can produce acid (Binkley and Giardina, 1997; Tang, 1997; Tang *et al.*, 1997; Tang *et al.*, 1999) and acacia plantations are associated with increasing soil acidity (Yamashita *et al.*, 2008; Kasongo *et al.*, 2009; Schiavo *et al.*, 2009; Sang *et al.*, 2012). If the dominant form of N in soil is NH_4^+, as is typical under acacia, cation uptake exceeds anion uptake (Tang, 1997; Tang *et al.*, 1999). This excess uptake of cations leads to excretion of H^+ by plant roots, the mechanism by which plants regulate their charge balance (Haynes, 1990), and a decrease of rhizosphere pH (Tang, 1997; Tang *et al.*, 1997). Any nitrification in the soil would also enhance acidification (Tang, 1997). Soil pH in an *A. auriculiformis* plantation on sandy soils in Congo decreased from age 1 to 17 yrs and was significantly lower than in nearby savannah (Kasongo *et al.*, 2009). That this is a real effect is demonstrated by a reversal of this decline after conversion of *Acacia* plantations to non-legume cropping systems (Tahir *et al.*, 2009). The significantly higher EC in plantations than abandoned land (58.5 – 69.4 µS cm^{-1} *v.* 32.7 µS cm^{-1}) is most likely related to greater water use and hence drier soils and lower leaching in plantations.

Bulk density (BD) was significantly higher in abandoned lands than plantations (1.55 g cm^{-3} *v.* 1.36 – 1.42 g cm^{-3}). Bulk density commonly increases after deforestation (Lal, 1996a; Yüksek *et al.*, 2010), but decreases with time after reforestation, especially in the upper layers (Lal, 1996a). The increase comes from soil compaction and erosion induced by raindrop impact when vegetation cover is removed. Fine soils are lost leaving gravels which have higher specific gravity. The decrease of BD is associated with the role of vegetation in protecting the soil from raindrop impact and thereby mitigating against soil compaction, as well as facilitating enhancement of soil SOM, soil organism activity and root penetration which all loosen soil.

4.4.2. Soil properties change within a single short rotation

Soil nutrient dynamics in short-rotation forestry are affected by management practices and in these *Acacia* hybrid plantations there was an indication, although non-significant, of depletion of TC stock after planting. This is often associated with afforestation but normally followed by recovery (Paul *et al.*, 2002), as also occurred by age 5 yrs in this study. Disturbance caused by land preparation and susceptibility of bare land to erosion when trees are small are the major reasons for the initial decline (Paul *et al.*, 2002). This was illustrated in the examination of the relationships between TC (%) or TN (%) and clay content. The lack of correlations at age 1.5 yrs (P>0.05; r^2=0.001 and 0.008, respectively) are possibly related to the effects of erosion being at a maximum following a period of little or no tree coverage. After canopy closure, which occurs at around age 2 yrs, the relationships became significant.

An observed trend of nutrient recovery in later years of the rotation, although only TN stock (Mg ha^{-1}) was significant, indicates that some enhancement of nutrient availability may occur in a longer rotation. In a previous study, TC (%) and TN (%) in soils of an *A. auriculiformis* plantation increased significantly after 4 yrs, and doubled after 8 yrs; exchangeable cations increased significantly after 10 yrs (Kasongo *et al.*, 2009). In 23- and 24-yr-old *A. mangium* plantations in South China, concentrations of TC and TN between 0 – 20 cm soil depth were substantially higher than in this study, 2.11 – 5.58% and 0.103 – 0.104%, respectively (Yang *et al.*, 2009; Wang *et al.*, 2010a). Thus while some elements are just maintained in a short rotation of tropical *Acacia* species, marked increases may happen over a longer rotation.

4.4.3. Nutrient stocks in gravelly soils

In this study, gravels > 2 mm represented 30 – 42% and 47% of the total soil mass for plantations and abandoned land, respectively. Correcting for gravel content resulted in significant differences in some element stocks between plantations and abandoned land, in particular TC at ages 0.5, 1.5, 2.5 and 5 yrs and TN at age 0.5 yr, whereas they were not significant for element concentration, except for TC at age 5 yrs. This also resulted in the different trends of changes with plantation age between element stocks and concentrations. Which is the better measure of soil nutrients in plantations, stock or concentration? While nutrient concentration provides a direct measure of soil nutrient availability for plant uptake, this is only the case if there is no between-root competition for, and free access to, available nutrients. In dense fast-growing species plantations, where plant roots have limited space and must compete for nutrients, nutrient stock is a better measure of available soil nutrients (Gersani *et al.*, 2001; O'Brien and Brown,

2008). Therefore in gravelly soils, nutrient accounting should be represented by nutrient stock after correcting for gravel content.

4.4.4. Tree growth and soil fertility

Although nutrient stocks and concentrations in the soils were extremely low, tree growth rates were high, with MAI of 28.7 m^3 ha^{-1} yr^{-1} by the end of a 5-yr rotation. However, correlations between soil properties and tree growth were largely absent. This suggests that the initial condition of the soils used in this study, particularly with respect to the key plant nutrients, were relatively similar among sites except for the factor of elevation which did appear to slightly effect DBH and height growth (P<0.05, r^2=0.094 and 0.16, respectively). Thus the differences in current soil properties between plantations and abandoned lands were clearly related to the acacia plantations rather than local variations in the initial soil properties.

4.5. Conclusion

We conclude that short-rotation *Acacia* hybrid plantations on degraded lands can either increase or conserve some key soil chemical and physical properties. However, levels of soil acidification of Acrisols dominated by sand remain high. Most soil properties were not significantly changed within a 5-yr rotation despite consistently observed trends of depletion in the first 2 – 3 yrs and later recovery after that in some key nutrients. This suggests potential for further improvements in some soil properties over a longer rotation. Soil nutrients are clearly related to some initial soil and site factors such as

gravel, clay content and elevation. In soil with a high proportion of gravel content, element stock per unit volume should take this factor into account, and provide a better measure of soil element levels than concentration.

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Fieldwork in *Acacia* hybrid plantations in Thua Thien Hue province.

Photo: Tran Lam Dong, July, 2010.

Chapter 5

GROWTH AND PHYSIOLOGY OF *HOPEA ODORATA* ROXB. PLANTED WITHIN CIRCULAR GAPS IN AN *ACACIA* HYBRID PLANTATION

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Abstract

Mixed-species plantations comprising tropical acacia nurse crops and various understorey native species have been established to aid forest restoration in Vietnam, but with limited success. Knowledge of the physiological mechanisms underlying competitive interactions between dipterocarp species and nurse crops remains limited, particularly in a plantation context. Seedlings of *Hopea odorata*, a shade-tolerant dipterocarp, were planted in three 22 m-diameter gaps within a 3-yr-old *Acacia* hybrid plantation in Central Vietnam. Growth and physiological responses to the environmental gradient created in these gaps were examined. Two years after establishment, stem diameter, total height and crown diameter of the *H. odorata* increased significantly from 1 m (G-1) outside the gap perimeter (GP) to the gap centre (GC). This positive response correlated with significant increases in daily incident photosynthetically active radiation (PAR) from 24% to 61% of total incident PAR. Net photosynthetic rate at 1500 μmol m^{-2} s^{-1} (A_{1500}) and stomatal conductance (g_s) were significantly lower for trees in the G-1 treatment than those 9 m from the perimeter (G9), as was light-saturated photosynthesis (A_{sat}) at age 1 yr only; at age 2 yrs there were no differences in A_{sat}. Apparent quantum yield (Φ), dark respiration (R_{dark}), and photosynthetic biochemical parameters (V_{cmax} and J_{max}) were similar between treatments. Chlorophyll content, chlorophyll fluorescence (F_v/F_m), and leaf N and P concentrations were also unaffected by treatment. Nevertheless, specific leaf area was higher in the G-1 than other treatments. Despite the substantial difference in PAR between treatments, trees in the G-1 treatment received levels of irradiation >500 μmol m^{-2} s^{-1} for 12% of the day *v*. 38% at the GC. Significant reductions of leaf water potential (Ψ_{leaf}) at the end of the dry season in treatments close to the GP compared to those near the GC suggested a competition for water between *H. odorata* and the acacia nurse trees,

although pre-dawn Ψ_{leaf} remained >-0.5 MPa. Thus, despite being a species that regenerates naturally in shade, *H. odorata* quickly acclimates to much higher light environments. Successful re-establishment of *H. odorata* on degraded sites using *A.* hybrid as a nurse crop should be possible in Vietnam provided the high levels of shading and competition for water are managed.

Keywords: dipterocarp, gas exchange, light response, native species planting, nurse crop, shade tolerant, water competition

5.1. Introduction

In Vietnam, approximately 0.9M ha of mixed-species plantations have been established (MARD, 2011). Most comprise an exotic tropical acacia species which is used as the nurse crop and several target native species, the most popular being *Hopea odorata* Roxb. (Tam, 2007). However, up to half of these plantations have failed because the much faster growing acacias have suppressed the growth of *H. odorata* (Tam, 2007). Species interactions in mixed-species plantations can be either complementary, neutral or competitive (Forrester *et al.*, 2006), and the interactions between a given pair of species also change spatially and temporally as resource availability changes, such as in response to competition and as stands develop (Forrester, 2014). In the mixed acacia and *H. odorata* system in Vietnam, the dominant type of interaction has proven to be competitive (Tam, 2007). Minimising these competitive effects forms an essential part of ensuring the success of nurse-crop systems. This can be done by acquiring a thorough

understanding of the changing requirements for resource inputs of the target species with plant development.

Hopea odorata is a late successional tree species of the Dipterocarpaceae which requires shade and high soil moisture content for its natural regeneration (Bunyavejchewin *et al.*, 2003; Kettle, 2009). Nevertheless, its demand for light increases with age (Kamaluddin and Grace, 1993; Appanah, 1998), though how this variability in shade tolerance changes with plant development remains largely unquantified (Weinland, 1998). In a natural forest in southern Vietnam, seedlings of *H. odorata* required, on average, at least 11% of ambient incident photosynthetic active radiation (PAR, measured at 1.5 m above the forest floor) to initiate vigorous seedling development (Dong *et al.*, 2013); in a glasshouse experiment, seedling growth and photosynthetic rates responded positively up to 42% of ambient incident PAR (Lee *et al.*, 1997). There is also evidence that *H. odorata* can adapt to ambient light conditions by changing its foliar chemistry and structure (Lee *et al.*, 2000).

Shade- and sun-adapted plants are morphologically and physiologically distinct (Boardman, 1977; Givnish, 1988; Cao, 2000). Under different shading levels, leaves of *H. odorata* and *Hopea helferi* in deeper shade were thinner; this was associated with significantly thinner leaf mesophyll (Lee *et al.*, 2000), lower stomatal density (Lee *et al.*, 1997) and higher chlorophyll content per unit area, particularly chlorophyll b for capturing light at low intensities (Lee *et al.*, 2000; Phonguodume *et al.*, 2012). Shade-adapted leaves also have larger chloroplasts which are closer to the leaf surface, larger stomatal pore size, higher photosynthetic light-use efficiency (Boardman, 1977; Givnish, 1988), and lower light-compensation point and dark respiration (Eschenbach *et al.*, 1998) than sun plants. While sun-adapted plants tend to allocate photosynthate to height

growth, shade-adapted plants allocate more photosynthate to lateral growth in order to capture more light (Tilman, 1988; Oliver and Larson, 1990; Chen *et al.*, 1996; Chen, 1997). Thus, with decreasing light availability, plants allocate proportionately more above-ground biomass to leaves to increase leaf area (Chen *et al.*, 1996; Chen, 1997).

Tropical acacias are widely used as pioneer species for afforestation and reforestation (Turnbull *et al.*, 1998; Yang *et al.*, 2009; Wang *et al.*, 2010a), especially on degraded soils. With their capacity to fix atmospheric N_2 and high growth rates, a faster recovery of soil nutrient capital and acceleration of the nutrient cycle is offered compared to non-legume species (Binkley and Giardina, 1997; Resh *et al.*, 2002; Brockwell *et al.*, 2005; Forrester *et al.*, 2005b; Forrester *et al.*, 2007; Kasongo *et al.*, 2009; Schiavo *et al.*, 2009; Wang *et al.*, 2010a). Their rapid canopy closure buffers the microclimate and reduces incident levels of solar radiation in the understorey, potentially providing suitable conditions for the establishment of shade-adapted species (Norisada *et al.*, 2005; Yang *et al.*, 2009) like *H. odorata* and other dipterocarps. When used as nurse crops, they can prevent transplant shock, suppress invasive weeds and provide sidelight suppression, thereby enhancing the survival, growth and stem quality of target seedlings (Otsamo, 1998a; Medhurst *et al.*, 2003; Norisada *et al.*, 2005; McNamara *et al.*, 2006; Sakai *et al.*, 2009; Yang *et al.*, 2009). These facilitative effects make tropical acacias particularly suitable for the reintroduction of native species into environments that have been compromised by unsustainable harvest- and land use-practices (Dong *et al.*, 2014). However, these benefits can be short-lived as their very high growth rates may quickly lead to excessive levels of shade and competition for soil water and nutrients (McNamara *et al.*, 2006; Tam, 2007).

While some studies have examined physiological responses of *H. odorata* to different light environments, there is currently no information on its physiological responses to interspecific competition in species mixtures. Sakai *et al.* (2009) reported higher growth rates of *H. odorata* when grown in monoculture or with the sparer canopy *Senna siamea* than with *Acacia auriculiformis* or *Eucalyptus camaldulensis*, and concluded that these differences were linked to light environment only. Nevertheless, it is recognised that competition for below-ground resources, such as soil moisture (Norisada *et al.*, 2005), between the nurse crop and *H. odorata* may also compromise growth of the native species. The high growth rates of tropical acacias are associated with high rates of water consumption due to high sap flow and canopy transpiration (Cienciala *et al.*, 2000) as well as low water-use efficiency and high moisture content of the stem (Yamamoto *et al.*, 2003; Inagaki *et al.*, 2008). Nutrient uptake by the acacia is also likely to be high to satisfy its fast growth rate, and this may also affect the growth of the target trees.

To date, the majority of physiological studies of dipterocarps have been conducted in covered shade-houses or under the canopy in natural forests where the pattern of receipt of incoming radiation in terms of light duration, light intensity and frequency differs from that in a large gap (Chazdon and Fetcher, 1984). While such studies explain the performance of shade-tolerant species in the environment dominated by sunfleck, the effects of much longer periods of high irradiation on the growth, leaf development and physiological performance of native target trees need to be examined (Leakey *et al.*, 2003a, b; Leakey *et al.*, 2005).

This study examined the growth and physiological responses of *H. odorata* seedlings planted in circular gaps created in a 3-yr-old *Acacia* hybrid plantation. A

gradient of decreasing interspecific competition for light, water and nutrients from the gap perimeter to the gap centre was used to answer the following questions: (1) how does the growth of the *H. odorata* seedlings respond to different levels of interspecific competition which are decreasing from gap perimeter to gap centre; and (2) can these growth responses be explained by changes in ecophysiological traits related to leaf-level gas exchange, leaf nutrients and tree water status?

5.2. Materials and methods

5.2.1. Location, climate and soil

The study site was located at Phu Loc, Thua Thien Hue province in Central Vietnam (lat. 16.3°N, long. 107.7°E, and 25 m altitude). The climate is monsoonal with a distinct wet season (September to December) associated with typhoons, and a long dry season (January to August). Mean annual rainfall is >3500 mm; mean annual and lowest and highest mean monthly temperatures are 24.9 °C, 19.4 °C (January) and 29.3 °C (June), respectively; mean air humidity is 86.8% (Hue weather station, unpublished data) (Fig. 5.1). The soil is a predominantly siliceous and sandy acrisol (Sang *et al.*, 2012), with high proportions (ca. 25%) of weathered coarse fragments (>2 mm) derived from granite, sandstone and gritstone (Que *et al.*, 2010). Concentrations in soils of total carbon (0.82%) and all nutrients are low: total nitrogen (0.06%), extractable phosphorus (2.42 mg kg^{-1}), and exchangeable potassium (0.01 cmol kg^{-1}), calcium (0.50 cmol kg^{-1}), magnesium (0.13 cmol kg^{-1}), and sodium (0.11 cmol kg^{-1}) (Table 5.1), and probably related to the low clay (14%) and high sand (83%) contents. The soil is acidic with pH_{CaCl2} of 3.8 and pH_{H2O} of 4.3 (Table 5.1).

Table 5.1 Soil properties at the experimental site at Phu Loc, Thua Thien Hue, Central Vietnam (mean ± 1 SD, n = 6)

Properties	Value
Total C (%)	0.82 ± 0.23
Total N (%)	0.06 ± 0.02
Ext-P (mg kg^{-1})	2.42 ± 1.25
Ex-K (cmol kg^{-1})	0.01 ± 0.003
Ex-Ca (cmol kg^{-1})	0.50 ± 0.36
Ex-Mg (cmol kg^{-1})	0.13 ± 0.04
Ex-Na (cmol kg^{-1})	0.11 ± 0.07
pH_{CaCl2} (1:5)	3.78 ± 0.09
pH_{H2O} (1:5)	4.29 ± 0.10
BD (g cm^{-3})	1.48 ± 0.08
Clay (%)	13.8 ± 5.3
Sand (%)	82.7 ± 7.2

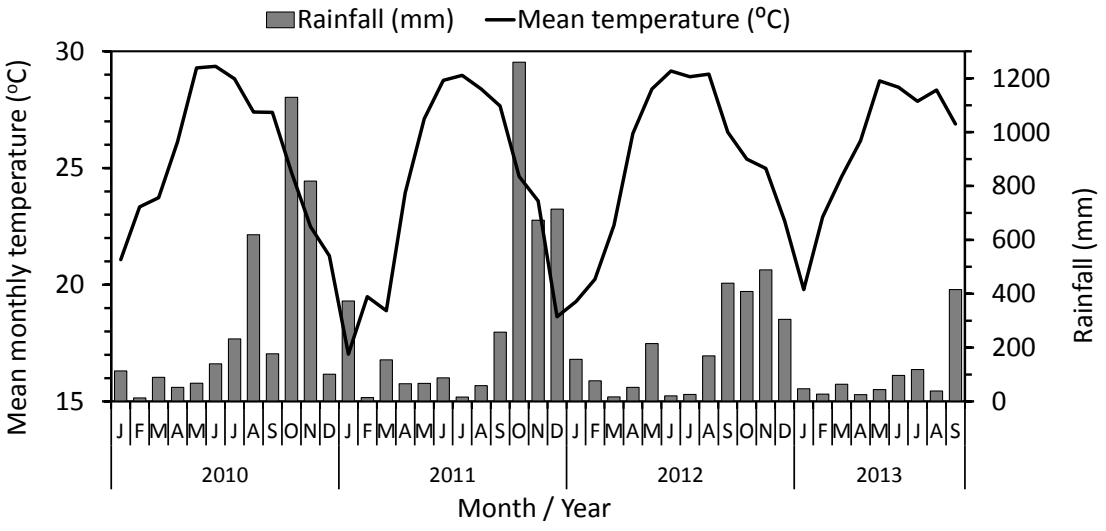

Figure 5.1 Mean monthly temperature (°C) and rainfall (mm) at Hue weather station (20 km from the experimental site) (National Centre for Hydro-meteorological Forecasting, 2013)

5.2.2. Experimental design

The *Acacia* hybrid nurse trees were planted in October 2008 at a spacing of 2 × 2 m. The experiment was established in September 2011, at the start of the wet season, when diameter at breast height ($D_{1.3A}$; cm), mean top height (H_{tA}; m), crown length (L_{cA}; m) and crown diameter (D_{cA}; m) of the *Acacia* hybrid were 7.7 cm, 10.5 m, and 3.85 m and 1.96 m, respectively (Table 5.2). Three circular gaps, each 22 m in diameter, were created within the plantation by cutting all trees inside the perimeter; the harvested stems were removed and the leaves and branches retained on site. Sixteen-month-old seedlings of *Hopea odorata* of mean height and diameter at 5 cm above ground of 0.87 m and 0.67 cm, respectively, were then planted at a spacing of 2 × 2 m within the gaps.

For light and growth measurements, seven treatment positions were established based on the radial distance from the gap perimeter (GP) to the gap centre (GC which was 11 m from the GP), viz -1 m (G-1), 1 m (G1), 3 m (G3), 5 m (G5), 7 m (G7), 9 m (G9) and 11 m (GC) from the GP, along each of the four cardinal directions N, S, E and W. For leaf area and physiological measurements of *H. odorata*, four treatments were established based on the radial distances -1 m (G-1), 3 m (G3), 6 m (G6) and 9 m (G9) from the GP along the same directions. Light, leaf area and physiological measurements were undertaken in one randomly selected gap.

5.2.3. Light transmission

The gradient of transmitted photosynthetically active radiation (PAR) was measured in August 2012. Twenty-five quantum sensors (Delta-T Devices QS2 400 and 700 nm) were horizontally mounted at 1.5 m height above ground at each of the treatment

positions, with one sensor at the GC. The sensors were connected to a data logger (Campbell Scientific CR1000 through an AM416 multiplexer) between 8th and 20th August 2012. PAR (μmol m^{-2} s^{-1}) was recorded automatically every 5 min as the average of data taken every 30 s; total incident PAR was similarly recorded from three quantum sensors located in an open area 1 km from the site. The PAR in each treatment was calculated as relative daily transmitted PAR (%).

5.2.4. Growth and specific leaf area

Size and form of all *H. odorata* saplings in the three gaps were recorded in August 2012 and 2013, approximately one and two years after planting, and their radial distance from the GP noted for classifying into the seven different treatments. The variables recorded were diameter at 0.3 m ($D_{0.3H}$; cm) and $D_{1.3H}$ (age 2 yrs only), total height (H_{tH}), crown length (L_{cH}) and crown diameter (D_{cH}). Stem form was assessed based on straightness (four levels), damage (three levels) (Maria Ottenschlaeger, pers. comm.), and numbers of competing apical leaders.

For determination of specific leaf area (SLA) in each year of measurement, three trees were selected for sampling in each of treatments G-1, G3, G6 and G9. The selected trees in each treatment were one mean tree, one of +1 standard deviation (SD) and one of –1 SD, based on $D_{0.3}$ and H_t; the trees used differed between the first and second year. The canopy of each sample tree was divided equally into upper and lower zones of equal length. A sub-sample of 20 leaves representing the range of leaf sizes and ages was collected from each crown zone of each sample tree for SLA measurement. As some trees were used for gas-exchange measurements, collection of these sub-

samples occurred after their completion. Leaves were scanned (Canon Scanner Lide 210) and leaf area was determined using CAN-EYE V6.3.3 software. Each sub-sample was then dried to constant weight at 65^{o}C and SLA calculated for each crown zone as leaf area per leaf mass (cm^2 g^{-1}). The same sub-samples were used for analysis of leaf nitrogen (N_{leaf}) and phosphorus (P_{leaf}) concenration.

5.2.5. Physiological variables

5.2.5.1. Gas exchange

Gas-exchange measurements were undertaken at ages 1 and 2 yrs in the early wet season between 30th August and 4th September, 2012, and 3rd and 8th August, 2013, respectively. Except on days of significant rain and to ensure no effect of water stress on physiological performance, irrigation was applied evenly over the gap area every two days for ten days before measurements were taken; approximately 140 mm of irrigation/rainfall was received in the ten-day period. The replicates along each of the four cardinal directions were selected by choosing trees closest to the quantum sensor positions. Only the youngest fully-expanded leaves in the middle to upper zone of the crown on the sunlit side of the tree were selected for measurement.

Diurnal gas-exchange rates were determined on two leaves from each tree at approximately 2.5-h intervals between 0630 and 1800 h local time. Net light-saturated photosynthesis (A_{1500}) and stomatal conductance (g_s) at a PAR of 1500 μmol m^{-2} s^{-1} and an ambient CO_2 partial pressure (C_a, μmol CO_2 mol^{-1} air) of 400 μmol mol^{-1} were measured by a portable photosynthesis system incorporating CO_2 and H_2O infra-red gas analysers (Li-Cor LI-6400XT; Li-Cor, Lincoln, NE, USA) with CO_2 control and the

standard 20 × 30 mm chamber equipped with blue-red light emitting diodes (Model 6400-02B). As it took 1.5 – 2 h to measure all 16 trees, the order of measurement in each cardinal direction was chosen randomly on each measurement occasion.

Light response curves were made on a single leaf of each tree between 0900 – 1300 h local time; photosynthetic rates were recorded using the following sequence of PAR: 2000, 1500, 1000, 650, 300, 200, 100, 50 and 0 μmol m^{-2} s^{-1}, and at a C_a of 400 μmol mol^{-1}. Photosynthetic CO_2 response curves, the response of A_{1500} to intercellular CO_2 partial pressure (C_i, μmol CO_2 mol^{-1} air), was measured at age 2 yrs only. Measurements were also made on a single leaf of each sample tree between 0900 – 1300 h local time with C_a changing in the following sequence: 390, 300, 200, 150, 100, 0, 390, 450, 600, 800, 1000, 1500 and 2000 μmol mol^{-1}, and at an incident PAR of 1500 μmol m^{-2} s^{-1}. For both sets of curves, leaf temperatures varied between 29.5 and 31.5°C; vapour pressure deficit based on leaf temperature (VPD_L) approximated ambient conditions, varying between 1.3 and 2.5 kPa.

5.2.5.2. Leaf water potential (Ψ_{leaf})

Leaf water potential (Ψ_{leaf}) was measured at the end of the dry season (July 2013) and early in the wet season (September 2013) at approximately 2.5-h intervals from 0430 (pre-dawn) – 1800 h local time. Measurements were made on the same sample trees as those used for gas-exchange. At each time interval, a single leaf was removed from each tree, placed immediately into a sealed plastic bag and kept in a cool box in the dark until measurement was made within 15 min of excision using a 7 MPa pressure chamber (PMS Instruments Co., Corvallis, Oregon, USA).

5.2.5.3. Leaf nutrient and chlorophyll analyses

At ages 1 and 2 yrs, N_{leaf} and P_{leaf} concentrations were determined from finely-ground (IKA-WERKE, Malaysia) leaf sub-samples that were digested in sulphuric acid and hydrogen peroxide. Digested samples (~ 0.5 g) were colourimetrically analysed for *N* by the Kjeldahl method using a UDK 149 automatic distillation unit (VELP Sciencetifica, Italia) and for *P* by a UV-visible spectrophotometer (V-630, Jasco, USA).

At age 2 yrs only, three leaves from each tree used for gas-exchange were collected and stored on ice. Three 2 × 2 cm sections were cut from each leaf, ground manually and extracted in 98% acetone for 24 h (Ma *et al.*, 2013). Absorption of the extracts was measured at 644.8 and 661.6 nm using a UV-visible spectrophotometer (UV-2450, Shimadzu, Japan). Concentrations (μg ml^{-1}) of Chl a and Chl b were calculated (Ma *et al.*, 2013) and then converted to concentration per leaf area (μg cm^{-2}).

5.2.5.4. Chlorophyll fluorescence

Trees selected for gas-exchange measurement were used at the same time to measure maximum quantum yield of photosystem II (F_v/F_m) using a portable chlorophyll fluorometer (FluorPen FP 100 – Photon System Instrument PSI). Measurements were undertaken pre-dawn after dark adaptation overnight for three leaves in each treatment including the two leaves used in the gas-exchange measurements.

5.2.6. Data analysis

PAR data were used to determine daily frequency distribution of 5-min averages of PAR over light intensity classes; one overcast day (PAR <500 μmol m^{-2} s^{-1} throughout

the day) was excluded from this analysis. The start and end of the day was based on the PAR from the reference sensors. The frequency distribution of 5-min averages of PAR was grouped into five light intensity classes: 0-50 μmol m^{-2} s^{-1}, 50-250 μmol m^{-2} s^{-1}, 250-500 μmol m^{-2} s^{-1}, 500-1500 μmol m^{-2} s^{-1} and >1500 μmol m^{-2} s^{-1}.

A non-rectangular hyperbolic function was used to examine the relationship between photosynthetic rate and PAR (Sands, 1995) and to estimate apparent quantum yield (Φ), the light-saturated value of A (A_{sat}) and apparent dark respiration (R_{dark}). Photosynthetic responses to C_i were fitted to a biochemical model (Farquhar *et al.*, 1980; Caemmerer and Farquhar, 1981). The biochemical reaction parameters in this model (Caemmerer, 2000), V_{Cmax} and J_{max} were estimated from the fitting protocol in an Excel workbook on the Elsevier Resources website (http://www.elsevierdirect.com/companion.jsp?ISBN=9780123744609) that accompanies (Landsberg and Sands, 2011). The standard errors of, and correlations between, the estimated parameters were obtained using the NonlinXL software which is also available from the PhysEcol website.

SPSS version 21 was used for all statistical analysis. One-way ANOVA was used to compare means of PAR, growth, photosynthetic parameters, SLA of lower and upper crown zones, N_{leaf} and P_{leaf}, leaf pigments, and F_v/F_m in different treatments. The effects of treatment and time on the diurnal patterns of gas exchange, Ψ_{leaf} and WUE_i were examined by repeated measures ANOVA, accounting for the split-plot nature of the experimental design. LSD with Tukey adjustment for multiple comparisons was used to determine significant differences among treatments. Independent-sample t-tests were used to compare annual increment of growth parameters between two measurement times, and SLA between lower and upper crown zones. Relationships

between A_{1500} and pigment contents, A_{1500} and leaf N, A_{1500} and Ψ_{leaf}, and A_{1500} and g_s were examined by generalized regression.

5.3. Results

5.3.1. Nurse crop and light condition

5.3.1.1. Growth of Acacia *hybrid*

At planting of *H. odorata* in September 2011, the stocking density of the *Acacia* hybrid nurse crop was 2,160 trees ha^{-1}; mean $D_{1.3A}$ was 7.7 cm, H_{tA} was 10.5 m, L_{cA} was 3.9 m and D_{cA} was 2.0 m (Table 5.2). In August 2012 and August 2013, $D_{1.3A}$ was 9.7 and 10.8 cm, H_{tA} was 14.7 and 17.3 m, L_{cA} was 4.0 and 4.2 m and D_{cA} was 2.2 and 2.2, respectively.

Table 5.2 Stem diameter ($D_{1.3A}$), total height (H_{tA}), crown length (L_{cA}) and crown diameter (D_{cA}) of the *Acacia* hybrid nurse crop (mean ± 1 SD, n = 121) during the experiment

Activity	Month/ Year	Stand density (trees ha^{-1}) (m × m)	$D_{1.3A}$ (cm)	H_{tA} (m)	L_{cA} (m)	D_{cA} (m)
Planting *A.* hybrid	10/2008	2,500 (2 × 2)				
Planting *H. odorata*	9/2011	2,160	7.7 ± 1.8	10.5 ± 1.4	3.9 ± 1.1	2.0 ± 0.4
1st yr measurement	8/2012	2,160	9.7 ± 2.0	14.7 ± 1.9	4.0 ± 1.2	2.2 ± 0.6
2nd yr measurement	8/2013	2,160	10.8 ± 2.4	17.3 ± 2.2	4.2 ± 1.4	2.2 ± 0.5

5.3.1.2. Light gradient across circular gap

Relative daily transmitted PAR increased significantly from 24% just outside the gap perimeter (G-1) to 59% at 7 m from the perimeter (G7), and was not significantly different between G7 and the G9 (Table 5.3). There was a sharp increase of mean PAR at 0900 h and decrease at 1400 h in treatments between G5 and GC; other treatments increased and decreased more evenly (Fig. 5.2). At noon, mean PAR at the GC was lower than mean total incident PAR (1400 μmol m^{-2} s^{-1} *v.* 1670 μmol m^{-2} s^{-1}) (Fig. 5.2).

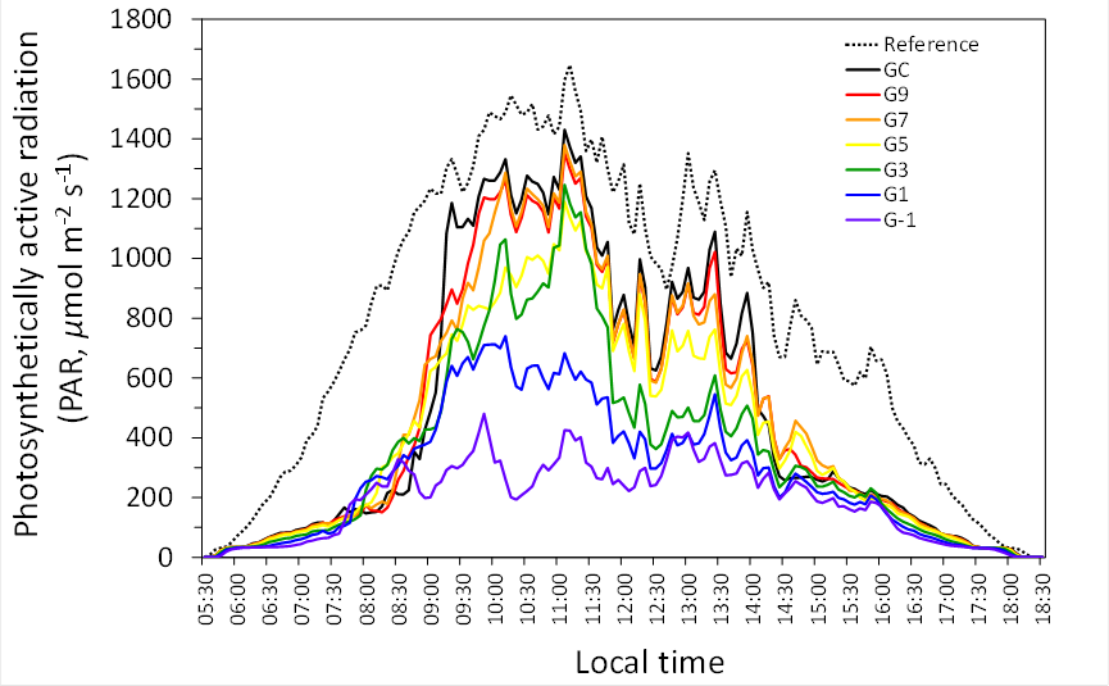

Figure 5.2 Diurnal changes of mean photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}) between 8th and 20th August 2012 across the 22-m circular gap in the 4-yr-old *Acacia* hybrid plantation (mean, n = 4 for all treatments except n = 1 for G11 and n = 3 for Reference outside plantation). Treatments, G-1, G1, G3, G5, G7, G9 and GC, were respectively -1, 1, 3, 5, 7, 9 and 11 m from the gap perimeter

The reference sensors detected a significantly lower proportion of PAR at <250 μmol m^{-2} s^{-1} than all gap treatments; the reverse was the case at PAR >500 μmol m^{-2} s^{-1} (Fig. 5.3). Treatments G-1 and G1 had significantly higher proportions of PAR between 0-50 and 50-250 μmol m^{-2} s^{-1} than between G5-GC and G7-GC, respectively; conversely G-1 and G1 had significantly lower proportions of PAR between 500-1500 and >1500 μmol m^{-2} s^{-1} than between G7-GC and G5-GC. There were no significant differences among gap treatments between 250-500 μmol m^{-2} s^{-1}. Thus trees at G-1 received approximately 10% and 2% of the 5-min averages at intensities between 500 – 1500 μmol m^{-2} s^{-1} and >1500 μmol m^{-2} s^{-1} respectively; at the GC these were 24 and 14%, respectively.

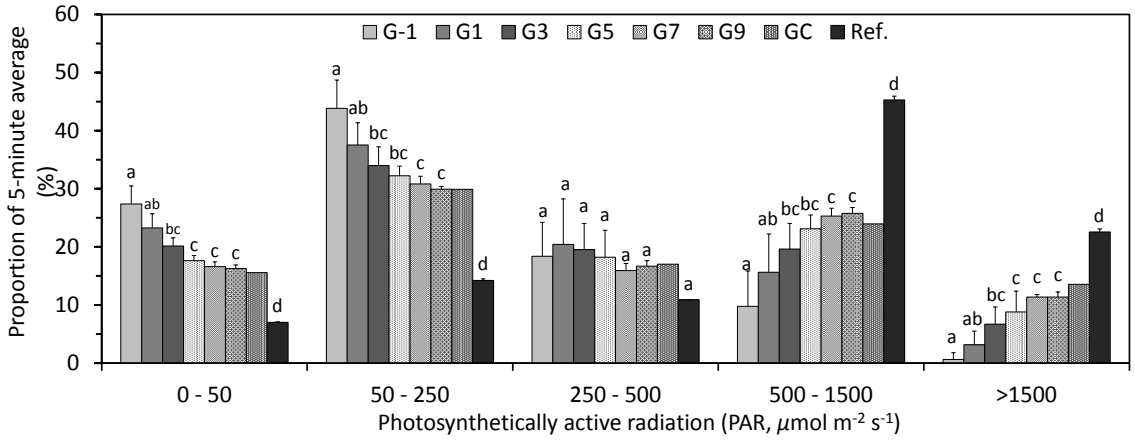

Figure 5.3 Distribution of five-minute averages of photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}) in different intensity classes (0-50, 50-250, 250-500, 500-1500 and >1500 μmol m^{-2} s^{-1}) on ten days between 9th and 20th August 2012 (data excludes one overcast day). The treatments are as described in Fig. 5.2. The same letter indicates that treatments are not significantly different at the 0.05 level with Tukey adjustment for multiple comparisons

5.3.2. Growth response of *H. odorata*

The patterns of growth of $D_{0.3H}$, H_{tH} and D_{cH} indicated an increase from the GP towards the GC which was more marked in the second than first year of growth (Fig. 5.4). At age 1 yr, annual increments of $D_{0.3H}$, H_{tH} and D_{cH} of *H. odorata* increased significantly from the G-1 to the G5 treatment, except H_{tH} which was not significantly different between the G-1 and G1 treatment; there were no significant differences between the G5 and G9 treatments (Table 5.3). At age 2 yrs, annual increments of $D_{0.3H}$, H_{tH} and D_{cH} increased significantly from the G-1 to G7 treatment, except H_{tH} between the G-1 and G1 treatment; there were no differences between the G7 and G9 treatments. Similar differences were observed for the increments of D_{cH} in each year of measurement.

The annual increment of $D_{0.3H}$ at age 1 yr was significantly greater than at age 2 yrs in the G-1, G1, G3 and G5 treatment, but significantly smaller in the G7 and G9 treatment (Table 5.3). The annual increment of H_{tH} was the same at both tree ages for the G-1 to G5 treatment, but at age 2 yrs, significantly higher in the G7 and G9 treatment. The annual increment of D_{cH} at age 1 yr was significantly higher than at age 2 yrs in the G-1, G1, and G5 treatment, but it was significantly lower in G9 treatment.

There was no significant difference in stem straightness, level of damage, and the number of multiple apical leaders among treatments (data not presented). Treatment significantly affected the height:diameter ratio (Table 5.3). At age 1 yr, $H_{tH}/D_{0.3H}$ ratio was significantly higher in the G-1 than in other treatments, and there was no significant difference between other treatments. At age 2 yrs, the ratio in G-1 treatment was significantly higher than in other treatments; it was not significantly different between other treatments, except the ratio in G7 was significantly lower than in the G1.

Table 5.3 Transmitted photosynthetically active radiation (PAR) and annual increment (1st and 2nd yr) of stem diameter ($D_{0.3H}$), total height (H_{tH}) and crown diameter (D_{cH}) of *Hopea odorata* planted in 22-m-diameter gap of a 3-yr-old *Acacia* hybrid plantation (mean ± 1 SD)

Treatment	PAR at 1-yr-old (%)[#]	Annual increment									
		N		$D_{0.3H}$ (cm)		H_{tH} (m)		D_{cH} (m)		H_{tH} / $D_{0.3H}$ ratio	
		1st yr	2nd yr	1st yr	2nd yr	1st yr	2nd yr	1st yr	2nd yr	1st yr	2nd yr
G-1	24.2 ± 6.4 a	81	74	0.47 ± 0.12 a*	0.35 ± 0.20 a	0.22 ± 0.13 a	0.20 ± 0.19 a	0.22 ± 0.12 a*	0.18 ± 0.15 a	1.20 ± 0.12 a	1.02 ±.11 a
G1	35.4 ± 7.4 ab	84	80	0.58 ± 0.13 b*	0.43 ± 0.25 a	0.30 ± 0.17 a	0.26 ± 0.19 a	0.31 ± 0.14 b*	0.26 ± 0.17 ab	1.13 ± 0.12 b	0.99 ±.12 ab
G3	45.4 ± 7.2 bc	78	74	0.72 ± 0.17 c*	0.57 ± 0.31 b	0.40 ± 0.25 b	0.37 ± 0.25 b	0.39 ± 0.15 c	0.36 ± 0.24 b	1.10 ± 0.14 b	0.95 ±.12 bc
G5	52.3 ± 8.0 cd	54	54	0.97 ± 0.20 d*	0.84 ± 0.32 c	0.63 ± 0.26 c	0.59 ± 0.25 c	0.57 ± 0.19 d*	0.47 ± 0.25 c	1.07 ± 0.15 b	0.93 ±.11 bc
G7	59.0 ± 1.0 d	39	39	1.01 ± 0.15 d	1.14 ± 0.35 d*	0.67 ± 0.19 c	0.78 ± 0.24 d*	0.59 ± 0.15 d	0.63 ± 0.31 d	1.06 ± 0.11 b	0.90 ±.11 c
G9	59.1 ± 1.7 d	20	20	0.96 ± 0.16 d	1.21 ± 0.27 d*	0.70 ± 0.27 c	0.82 ± 0.24 d*	0.55 ± 0.18 d	0.67 ± 0.21 d*	1.11 ± 0.13 b	0.92 ±.12 bc
GC	61.7 d										
Reference	100 ± 0.6										

ANOVA with Tukey adjustment was used for multiple comparisons; within a column the treatments, G-1, G1, G3, G5, G7, G9 and GC (-1, 1, 3, 5, 7, 9 m from gap perimeter and gap centre, respectively), with similar letter are not significantly different at the 0.05 level. Independent sample t-test was used to compare means of each treatment between 1st and 2nd yr; * indicates a significant higher mean of each growth parameter between 1st and 2nd yr. [#]N = 4 for G-1, G1, G3, G5, G7 and G9 treatment, N = 1 for the GC and N = 3 for the references; total daily PAR of the reference = 40.0 ± 0.2 mol m^{-2}

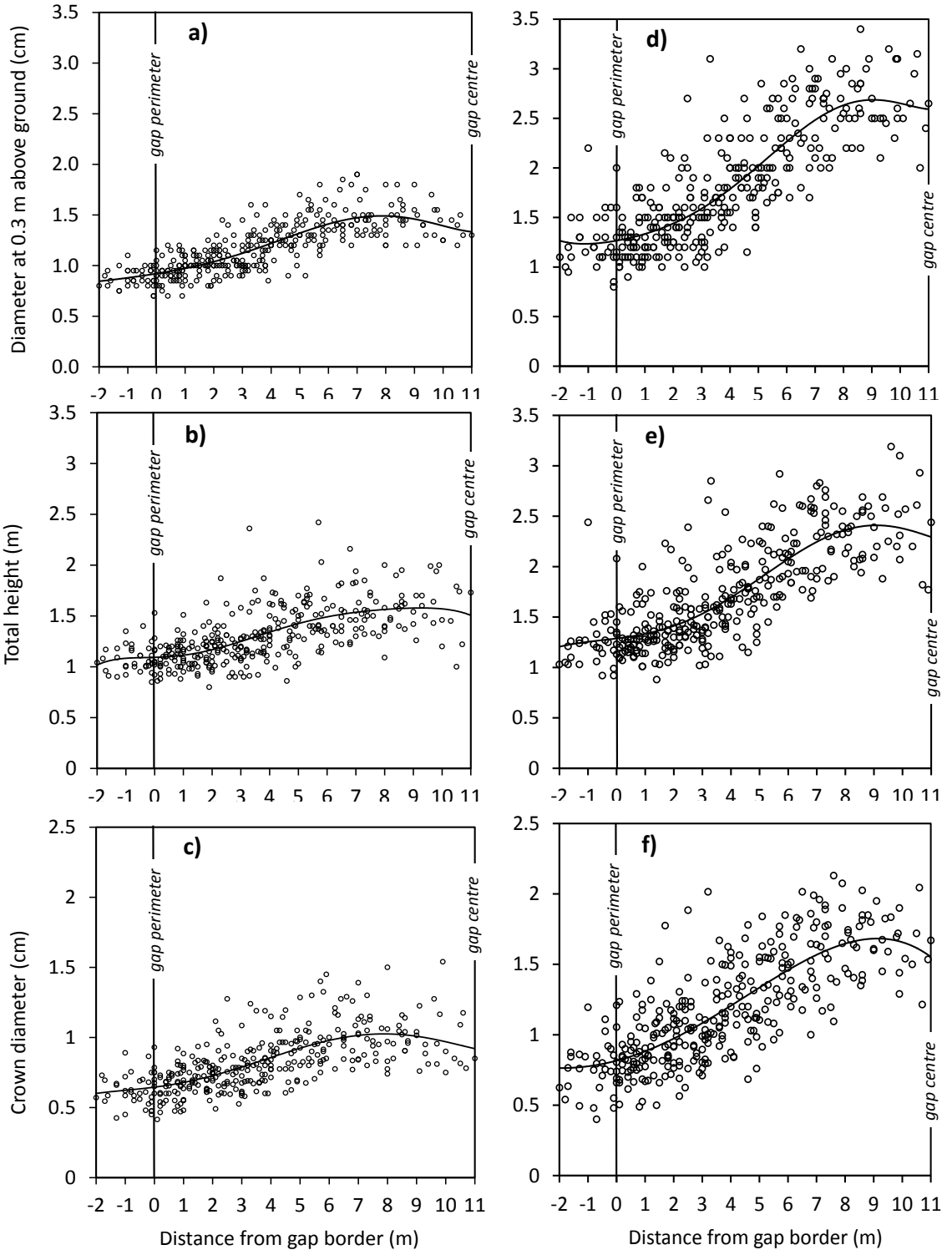

Figure 5.4 Diameter ($D_{0.3}$), height (H_t) and crown diameter (D_c) of *Hopea odorata* at age 1 (a, b, c) and 2 (d, e, f) yrs planted in a 22-m diameter gap within a 3-yr-old *Acacia* hybrid plantation (° observation, — mean fitted by quadratic equation)

5.3.3. Physiological response of *H. odorata*

5.3.3.1. Gas exchange

At ages 1 and 2 yrs, A_{1500} and g_s were significantly greater in the G9 than G-1 treatment; otherwise differences were not significant (Fig. 5.5). Diurnal changes in A_{1500} and g_s followed a consistent pattern for all treatments where high rates of A_{1500} were maintained between 0900 and 1400 h. Diurnal patterns of WUE_i were unaffected by gap treatment (Fig. 5.5). There was a significant positive relationship between A_{1500} and g_s at age 1 and 2 yrs, however this relationship was unaffected by gap treatment (Fig. 5.6).

The light-response curves showed that at age 1 yr, A_{sat} in G9 was significantly greater than in G-1; treatment had no significant effect on Φ and R_{dark} (Fig. 5.7; Table 5.4). At age 1 yr, light became saturating for A of the G-1 treatment when PAR was ~600 μmol m^{-2} s^{-1}; for the G9 treatment, it became saturating at ~1500 μmol m^{-2} s^{-1}; no differences were apparent at age 2 yrs (Fig 5.7). In the G-1 treatment, the effect of tree age on A_{sat} was significant; A_{sat} increased between age 1 and 2 yrs (Table 5.4). A_{sat} was similar at both ages in the G9 treatment. At age 2 yrs, R_{dark} was significantly greater than at age 1 yr for trees in the G-1 and G6 treatments (Table 5.4).

Neither V_{Cmax} nor J_{max} were influenced by gap treatments at age 2 yrs (Table 5.4).

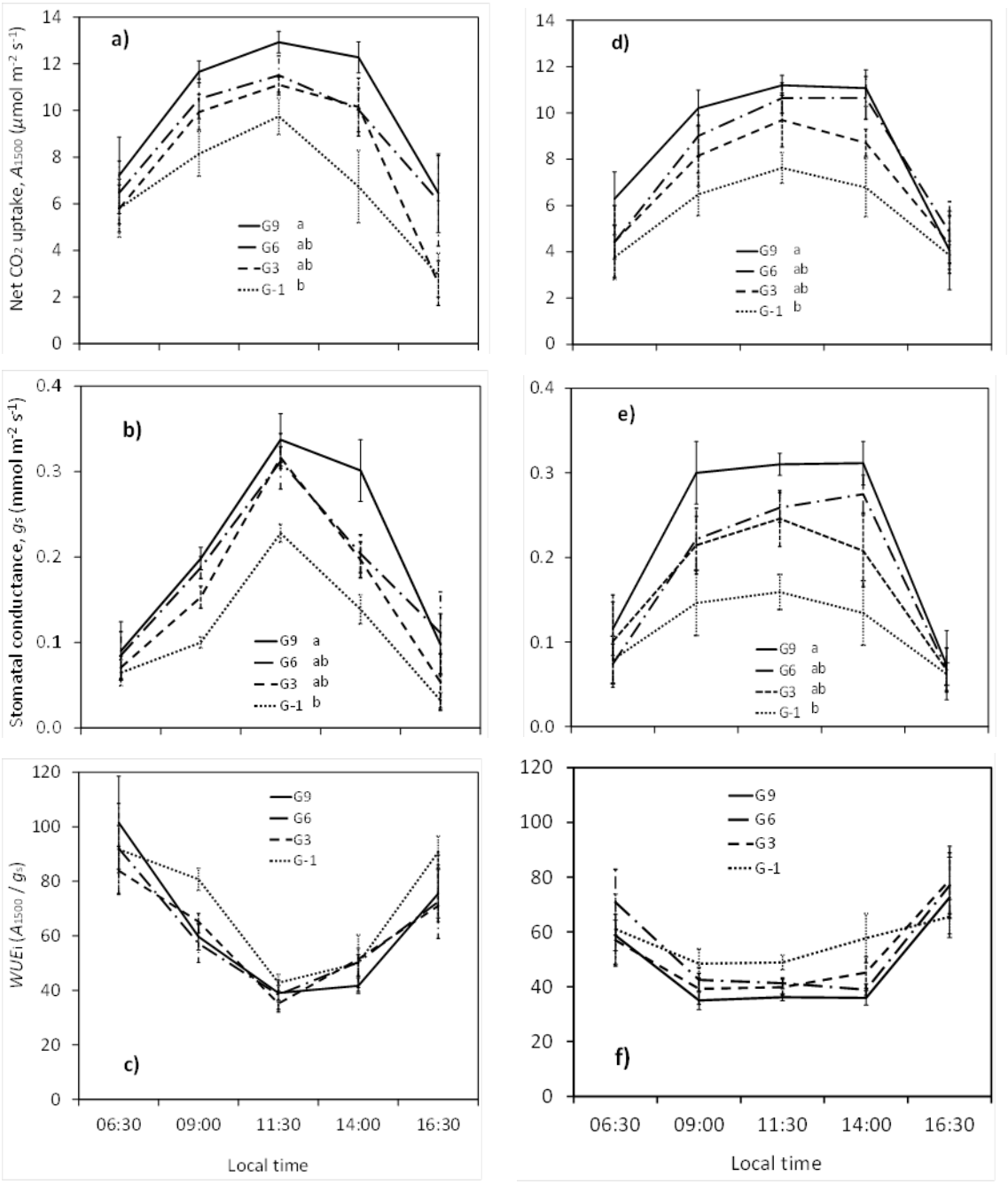

Figure 5.5 Light-saturated photosynthesis (A_{1500}), stomatal conductance (g_s) and intrinsic water-use efficiency (WUE_i, A_{1500}/g_s) of *Hopea odorata* at age 1 (a, b and c, respectively) and 2 (d, e and f, respectively) yrs planted in 22-m diameter gaps within a 3-yr-old *Acacia* hybrid plantation (mean ± 1 SE, n = 4). Treatments, G-1, G3, G6 and G9 (-1, 3, 6 and 9 m from the gap perimeter, respectively), with the same letter are not significantly different at the 0.05 level with Tukey adjustment for multiple comparisons

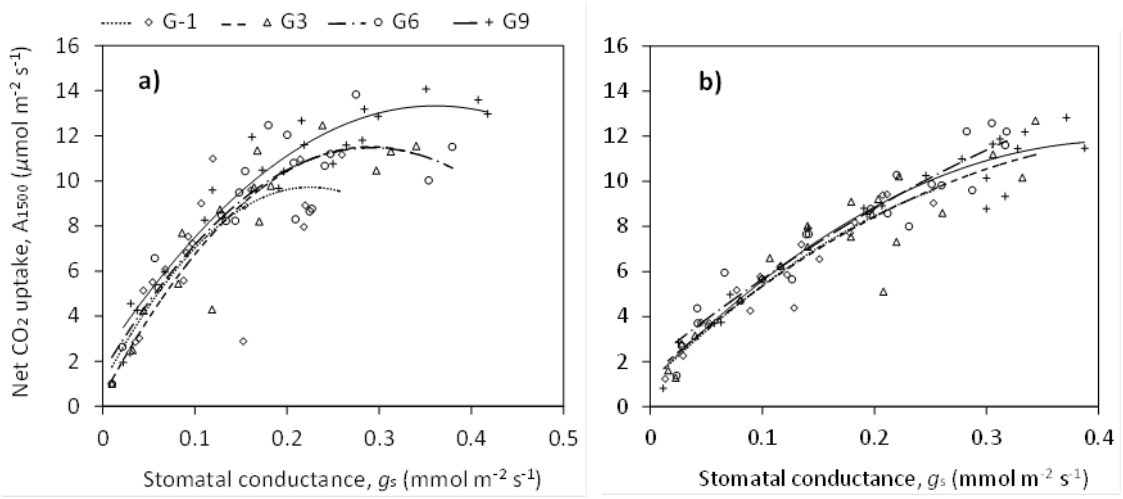

Figure 5.6 Relationship between light-saturated photosynthesis (A_{1500}) and stomatal conductance of *Hopea odorata* at age 1 (a) and 2 yrs (b) planted in a 22-m diameter gap within a 3-yr-old *Acacia* hybrid plantation. Models were fitted by a quadratic equation. Treatments, G-1, G3, G6 and G9, were -1, 3, 6 and 9 m from gap perimeter, respectively

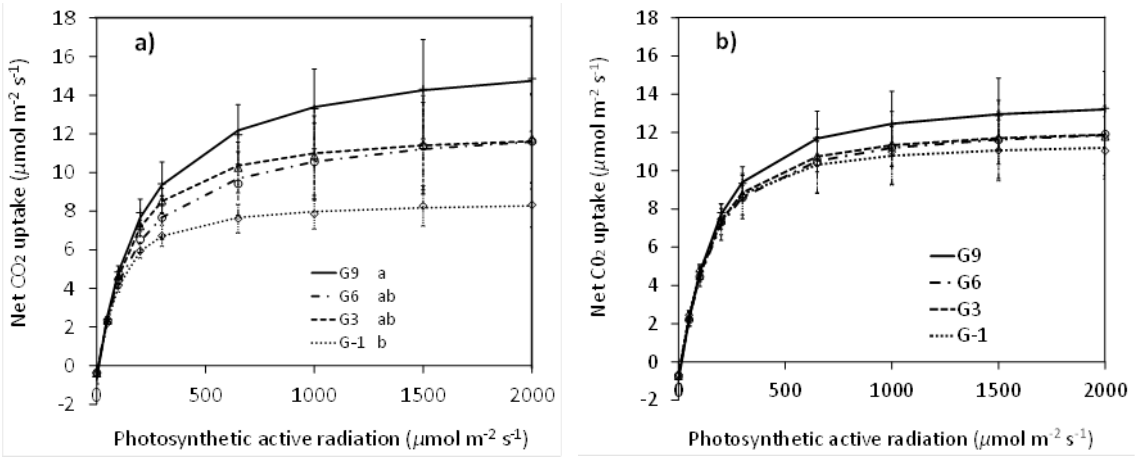

Figure 5.7 Photosynthetic light response curves of *Hopea odorata* at age 1 (a) and 2 yrs (b) planted in a 22-m diameter gap within a 3-yr-old *Acacia* hybrid plantation (mean ± 1 SE; n = 4). A non-rectangular hyperbolic function was used to fit relationship of net CO_2 uptake versus PAR (Sands, 1995). Treatments, G-1, G3, G6 and G9 (-1, 3, 6 and 9 m from gap perimeter, respectively), with the same letter in the legend are not significantly different at the 0.05 level with Tukey adjustment for multiple comparisons

Table 5.4 Parameters obtained from light-response and A-C_i curves of *Hopea odorata* at age 1 and 2 yrs planted in a 22 m diameter gap within a 3-yr-old *Acacia* hybrid plantation (mean ± 1 SD)

Treatment	1-yr-old			2-yr-old				
	$\Phi^{\#}$	A_{sat} (μmol m^{-2} s^{-1})	R_{dark} (μmol m^{-2} s^{-1})	Φ	A_{sat} (μmol m^{-2} s^{-1})	R_{dark} (μmol m^{-2} s^{-1})	V_{Cmax} (μmol m^{-2} s^{-1})	J_{max} (μmol m^{-2} s^{-1})
G-1 (n = 4)	0.065 ± 0.006	9.00 ± 1.27 a*	-0.43 ± 0.05	0.069 ± 0.004	12.27 ± 1.78	-0.67 ± 0.13*	40.3 ± 10.4	64.7 ± 6.1
G3 (n = 4)	0.067 ± 0.010	12.71 ± 2.81 ab	-0.45 ± 0.09	0.066 ± 0.004	13.09 ± 2.21	-0.67 ± 0.19	44.4 ± 5.7	63.4 ± 8.7
G6 (n = 4)	0.079 ± 0.016	13.46 ± 3.94 ab	-0.42 ± 0.10	0.069 ± 0.004	13.35 ± 2.09	-0.79 ± 0.13*	47.8 ± 5.0	68.5 ± 9.7
G9 (n = 4)	0.083 ± 0.009	17.15 ± 3.23 b	-0.70 ± 0.32	0.076 ± 0.009	15.01 ± 2.45	-1.02 ± 0.25	48.7 ± 3.6	78.0 ± 4.5

$^{\#}$ Light-response curve parameters of apparent quantum yield (Φ), light-saturated photosynthesis (A_{sat}) and dark respiration (R_{dark}) were estimated from the fitted non-rectangular hyperbolic functions of net CO_2 uptake versus PAR (Sands, 1995); A-C_i parameters V_{Cmax} and J_{max}, were fitted to a biochemical model (Caemmerer, 2000) in the Excel workbook that accompanies Landsberg and Sands (2011). ANOVA with Tukey adjustment was used for multiple comparisons; within a column the treatments, G-1, G3, G6, and G9 (-1, 3, 6, and 9 m from gap perimeter, respectively), with similar letters are not significantly different at the 0.05 level. Independent sample t-test was used to test for tree age effects on the means of each treatment; * indicates a significant higher mean of each parameter between ages 1 and 2 yrs

Table 5.5 Specific leaf area (SLA), leaf N and P (N_{leaf} and P_{leaf}), and photosynthetic pigment content (Chl a and b) of *Hopea odorata* planted in a 22-m diameter gap within a 3-yr-old *Acacia* hybrid plantation (mean ± 1 SD)

Treatment	SLA (cm^{-2} g^{-1}) at 2-yr-old			Leaf nutrient				Chlorophyll at 2-yr-old			
	N	Lower crown zone	Upper crown zone	N_{leaf} (mg g^{-1})		P_{leaf} (mg g^{-1})		N	Chl a		Chl b	
				1-yr-old	2-yr-old	1-yr-old	2-yr-old		μg cm^{-2}	mg g^{-1}	μg cm^{-2}	mg g^{-1}
G-1	3	133.9 ± 10.1 a*	127.1 ± 9.1 a	1.49 ± 0.16	1.35 ± 0.14	0.82 ± 0.05	0.67 ± 0.10	4	25.3 ± 8.8	1.49 ± 0.49	9.3 ± 4.4	0.55 ± 0.25
G3	3	122.6 ± 10.9 b*	113.6 ± 7.2 b	1.59 ± 0.15	1.55 ± 0.16	0.88 ± 0.08	0.74 ± 0.13	4	25.3 ± 6.4	1.42 ± 0.42	9.7 ± 2.7	0.55 ± 0.17
G6	3	120.1 ± 8.5 b	115.2 ± 7.3 b	1.53 ± 0.22	1.49 ± 0.18	0.83 ± 0.12	0.83 ± 0.32	4	31.3 ± 3.8	1.67 ± 0.30	12.4 ± 1.2	0.66 ± 0.06
G9	3	119.6 ± 14.1 b*	109.4 ± 10.8 b	1.66 ± 0.15	1.59 ± 0.18	0.85 ± 0.05	0.72 ± 0.10	4	25.8 ± 2.5	1.25 ± 0.10	10.2 ± 2.3	0.49 ± 0.10

ANOVA with Tukey adjustment was used for multiple comparisons; within a column the treatments, G-1, G3, G6, and G9 (-1, 3, 6, and 9 m from gap perimeter, respectively), with similar letter are not significantly different at the 0.05 level. * indicates a significant higher mean of SLA between lower and upper crown zone which was tested by independent sample t-test

5.3.3.2. Leaf morphology and chemistry

At age 2 yrs, SLA of the G-1 treatment was significantly lower than in other treatments; there were no significant differences among the other treatments (Table 5.5). Specific leaf area in the G-1, G3 and G9 treatments in the lower crown zone were significantly higher than in the upper crown zone.

At ages 1 and 2 yrs, treatment effects were not significant for N_{leaf} and P_{leaf} (Table 5.5).

At age 2 yrs, pigment content expressed as either per leaf mass or leaf area of chlorophyll a and chlorophyll b, as well as the total content were not significantly different among treatments (Table 5.5). The ratio of chlorophyll a/b (2.54 – 2.96) was similarly unaffected by treatment. The maximum photochemical efficiency of PS II was similar across treatments at age 1 yr (F_v/F_m, 0.785 – 0.794; data not presented).

5.3.3.3. Leaf water potential (Ψ_{leaf})

Diurnal patterns of Ψ_{leaf} were significantly influenced by season (Fig. 5.8). In the dry season, there were significant treatment effects; Ψ_{leaf} in the G-1 and G3 treatments was significantly lower than in G6 and G9 treatments. Minimum daily Ψ_{leaf} was reached at ~0900 h in the G-1 and G1 treatments (-2.14 MPa and -2.53 MPa, respectively) and at ~1400 h in the G6 and G9 treatments (-1.54 MPa and -1.66 MPa, respectively). In the wet season, there were no significant differences of Ψ_{leaf} among treatments (Fig. 5.8). In both seasons, pre-dawn Ψ_{leaf} across all treatments in both dry and wet seasons were not significantly different, and were >-0.5 MPa. Leaf water potential recovered between 1400 and 1630 h in all treatments and in both seasons.

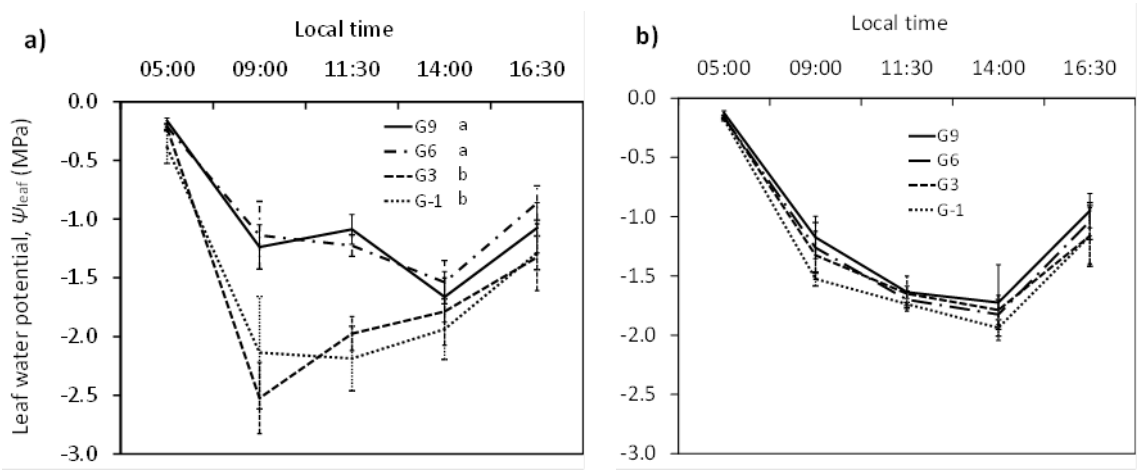

Figure 5.8 Diurnal changes of leaf water potential (Ψ_{leaf}, MPa) in the dry (a) and wet season (b) of *Hopea odorata* planted in a 22-m diameter gap within a 3-yr-old *Acacia* hybrid plantation (mean ± 1 SE; n = 4). Treatments, G-1, G3, G6 and G9 (-1, 3, 6 and 9 m from gap perimeter, respectively) with the same letter in the legend are not significantly different at the 0.05 level with Tukey adjustment for multiple comparisons

5.4. Discussion

The growth of *H. odorata* at ages 1 and 2 yrs was significantly influenced by the gap treatments created within an *A*cacia hybrid nurse crop. Previous studies have shown that *H. odorata* and some other dipterocarp species grow better under higher levels of available light (Otsamo, 1998a, 2000a; McNamara *et al.*, 2006; Sakai *et al.*, 2009). In this study, growth rates closely followed the distance from GP towards the GC which were associated with quantity of available light and leaf water status as it increased from the GP towards the GC. However, the difference in leaf water status only happened at the end of dry season, so the effect of light on growth could be much more important. This positive response to light availability suggests that *H. odorata*, which naturally regenerates in shaded environments, has a high phenotypic plasticity to incident light levels during seedling development. Even at the lowest light availability

just outside the perimeter, light saturation occurred at a much higher level than associated with shade-adapted leaves (Larcher, 2001 cited in Wittmann *et al.* (2005)). This suggests that seedlings of *H. odorata* are able to develop leaf traits which are more typical of sun- rather than shade-adapted species when planted with an *Acacia* hybrid nurse crop. Ther evidence of interspecific competition for water between *H. odorata* and the nurse crop may have modified the physiological responses to light availability. These issues are now discussed.

5.4.1. Effects of light availability

Photosynthetic rate (A_{1500}) and g_s of trees in the G-1 treatment just outside the GP were significantly lower than in the G9 treatment close to the gap centre. Differences in photosynthetic performance in response to light environment are usually related to adaptive changes in leaf anatomy and pigment content so that the leaves can optimise their physiological performance to incident light levels (Boardman, 1977; Lee *et al.*, 2000). However, treatment differences were unrelated to either chlorophyll or N_{leaf} content and there were no treatment differences in V_{Cmax} or J_{max}. Nevertheless SLA (m^{-2} g^{-1}) was significantly greater in the G-1 than the more well-lit treatments and in the lower than upper crown in most treatments, a common response to shade in all plants (Boardman, 1977; Chazdon and Kaufmann, 1993; Cao, 2000; Lee *et al.*, 2000). In *H. odorata* and *H. helferi*, greater SLA in shade- than sun-adapted plants was associated with significantly thinner palisade and spongy mesophyll and lower stomatal density (Boardman, 1977; Lee *et al.*, 2000). The last may have been responsible for the lower rates of stomatal conductance and photosynthesis in the G-1 treatment (Givnish, 1988). In common with other plants (Boardman, 1977; Givnish, 1988) shade-adapted leaves of

H. odorata have higher and lower total chlorophyll content per leaf mass and area, respectively, and lower chlorophyll a/b ratio than sun-adapted leaves (Lee *et al.*, 2000; Phonguodume *et al.*, 2012). Thus it appears that exposure to maximum incident levels of radiation for at least part of the day in the more shaded treatments in this study was sufficient to result in chlorophyll levels and ratios that were closer to those of more well-lit treatments.

This is supported by the distribution of 5-min averages of transmitted radiation which showed that gap treatments significantly influenced both the quantity and pattern of receipt of incident light. In spite of shading by *Acacia* hybrid, *H. odorata* seedlings in the G-1 treatment were exposed to radiation levels >500 μmol m^{-2} s^{-1} for 12% of the time which was approximately one-third of that received in the G9 treatment. It is probable that the way light is received by target species such as *H. odorata* planted into large gaps such as that created in this experiment and many nurse-crop systems differs from that received by regenerating seedlings in small gaps in the understorey of natural forest where sunflecks predominate (Coombe, 1957). In a tropical evergreen forest, sunflecks at the base of the canopy were usually of <2 min duration and the PAR rarely reached the equivalent of full-sun irradiation; conversely sun patches at a forest boundary or in more open forest may last up to some hours and PAR frequently reaches that of the full sun (Chazdon and Pearcy, 1991). As in this experiment where the gaps were 380 m^2 in area, a similar proportion of PAR between 100 – 500 μmol m^{-2} s^{-1} was received within 400 m^2 gaps in a tropical rainforest; within the closed forest, PAR was <10 μmol m^{-2} s^{-1} for >70% of the time, a condition which is more likely to lead to leaf traits more typical of shade-adapted plants (Chazdon and Fetcher, 1984).

The marked increase in physiological and growth performance from the GP to the GC shows that *H. odorata* is able to acclimate to increasing proportional levels of high irradiance. An examination of a number of dipterocarp species, though not *H. odorata*, growing in lowland natural forest in Malaysia showed that photosynthesis was saturated at PAR <500 μmol m^{-2} s^{-1} (Eschenbach *et al.*, 1998) and at values typical of shade-adapted leaves (200–500 μmol m^{-2} s^{-1}; Larcher, 2001 cited in Wittmann *et al.* (2005). In the current study, light saturation at age 1 yr in the G-1 treatment occurred at ~600 μmol m^{-2} s^{-1} and ~1000 μmol m^{-2} s^{-1} in the G9 treatment, providing strong evidence that *H. odorata* has capacity for developing physiological capacities associated with sun-adapted species which were fully consolidated by age 2 yrs when A_{sat} occurred at >1000 μmol m^{-2} s^{-1} in all treatments. This adaptation to higher incident levels of light was accompanied by greater A_{max} (8 – 13 μmol m^{-2} s^{-1}) than in studies where dipterocarp leaves were saturated at lower PAR (5 – 6 μmol m^{-2} s^{-1} (Eschenbach *et al.*, 1998) and 4 – 6 μmol m^{-2} s^{-1} (Lee *et al.*, 1997)). Ishida *et al.* (1999) showed that while net photosynthetic rate was higher in an open site than forest gap for the moderately shade-tolerant dipterocarp species *Shorea leprosula*, it was higher in a gap than open site for the obligate shade species, *Neobalanocarpus heimii*. Thus, in spite its natural regeneration occurs in shade, *H. odorata* appears capable of acclimation to high irradiation which is necessary for successful growth in a more open environment.

The positive response of growth and photosynthesis to increasing irradiance questions the accepted inherent light demand of *H. odorata*. Dipterocarps have long been considered shade tolerant, though how this varies with species and plant development is not well quantified (Weinland, 1998). In this study, the light levels tested varied between 24% and 60% total incident PAR as measured at the end of the first year. Annual increments of $D_{0.3H}$, H_{tH} and D_{cH} increased in this year of growth

between the G-1 and G5 treatments (24% to 52% PAR) and in the second year between G-1 and G7 treatments. This wider response may have been caused by the 2.6 m increase in height of the *Acacia* hybrid nurse crop during the second year resulting in greater levels of shade being experienced by all treatments. It may also partially affected by increasing light demand due to ontogenetic effect, as it was shown at age 2 yrs *H. odorata* at the G-1 position has a similar light response to the G9. In natural forest, a low light threshold of 11% total incident radiation was found for seedling development (Dong *et al.*, 2013). The reduced growth at the lower levels of incident light in the current experiment may therefore be part of a continuum related to light availability only or possibly light availability and interspecific competition for resources other than light. In spite of the very small and non-significant differences in levels of incident radiation between the G7 and G9 treatments (59.0%), a trend of declining of growth rate suggested by the quadratic relationships fitted to Fig. 5.4 suggests that an optimum level of radiation may have been reached, though the lack of difference in F_v/F_m between treatments shows that these higher levels of incident radiation were not associated with photosynthetic stress (Yang *et al.*, 2009). Reduced light availability and greater competition for other resources may also explain the significant reduction in the annual increment of $D_{0.3H}$ of treatments G-1 to G5 between age 1 and 2 yrs; conversely where competition was minimal near the centre of the gap, increments of $D_{0.3H}$ and H_{tH} increased between these ages.

Nurse crops are often associated with improvements in stem form of the target species because of sidelight suppression but compromise growth rate because of shading (Medhurst *et al.*, 2003). However in this study, while growth rate was reduced by shading, stem straightness, stem damage and the number of apical leaders of the *H. odorata* were unaffected by light condition. This suggested that partial shading in gaps

which receive up to 60% incident PAR results in equal levels of seedling/sapling stem quality. Gap treatment affected $H_{tH}/D_{0.3H}$ which decreased with increasing light intensity. Lower height:diameter ratio and shorter internodes were observed in *H. odorata* seedlings grown in full sunlight compared to shaded treatments (Lee *et al.*, 1997), suggesting that higher incident PAR than used in the current study may lead to negative effects on stem form.

5.4.2. Effects of gap treatment on leaf water and nutrient status

Previous field studies that have examined the growth of *H. odorata* planted with different nurse tree species have not examined whether interspecific competition for water and nutrients as well as light availability was affecting the observed growth response (McNamara *et al.*, 2006; Sakai *et al.*, 2009). In the current study, there was no interspecific competition for water in the wet season. In contrast, at the end of the dry season, Ψ_{leaf} was significantly lower up to 3 m from the GP than at 6 and 9 m from the perimeter. In natural forest, *H. odorata* is usually associated with wet sites (Bunyavejchewin *et al.*, 2003). Given that seedling growth has been found to be higher in well-watered *v.* water-limited treatments (Zainudin *et al.*, 2003) and unaffected by water-logging for up to 60 days (Abdul-Hamid *et al.*, 2009), there may be an expectation that *H. odorata* is sensitive to water stress. Secondly, as tropical acacias have been linked to high rates of sap flow and canopy transpiration (Cienciala *et al.*, 2000) and low water-use efficiency (Yamamoto *et al.*, 2003; Inagaki *et al.*, 2008), intense competition for water between the nurse crop and target species (Norisada *et al.*, 2005) is a likely reason for the development of low Ψ_{leaf} in *H. odorata* at the end of the dry season. Nevertheless, pre-dawn Ψ_{leaf} was always >-0.5 MPa in all treatments in both

dry and wet seasons indicating that *H. odorata* was still able to extract water from soils even under the driest conditions experienced. Therefore, the effects of water stress on the growth of *H. odorata* would likely have been less than the effects of shading though in the context of the current study they were not able to quantify.

Although the soils were very low in nutrient concentration, there was no evidence of nutrient competition between the *Acacia* hybrid and *H. odorata*. Leaves of *H. odorata* in all treatments showed no symptoms of nutrient deficiency and there were no significant differences in N_{leaf} and P_{leaf} among treatments. The demand for nutrients by dipterocarp seedlings during early establishment is small in the low light environments associated with gap regeneration in closed dipterocarp forest (Turner *et al.*, 1993), but this is anticipated to increase in less light-limited environments that support higher growth rates (Nussbaum *et al.*, 1995), such as those associated with the current study. Thus, while there was no evidence of nutrient limitation in the treatments close to GP, slow growth due to low light availability and water competition may have reduced the level of nutrient demand by *H. odorata*, thereby preventing any expression of potential nutrient stress.

5.5. Conclusion

This study has shown that growth of *H. odorata* is positively related to the decreasing interspecific competion from gap perimeter to gap centre. This is majorly because of the increasing light availability associated with increasing photosynthetic performance up to 60% incident PAR. While gap treatment affected light availability, light patterns resulted in trees in all treatments being exposed to high irradiation for a proportion of

the day. This resulted in gas-exchange, and foliar chemistry and structure being more akin to sun-adapted leaves. Low Ψ_{leaf} close to the GP at the end of the dry season indicated that the growth of *H. odorata* was also affected by interspecific competition for soil water, though this did not appear to be severe in this high annual rainfall area. Therefore, using acacias as nurse crops for re-establishment of *H. odorata* on degraded lands should be possible, provided that the negative effects of interspecific competition are managed. Examination is now necessary of how crown architecture of *H. odorata* responds to further changes of available light with gap condition and stand development, and how this affects tree growth and stem form until the bole is fully formed.

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Hopea odorata when planted in the circular-gap experiment, Sep. 2011

Gas-exchange measurement by Licor 6400XT, Aug. 2013. Photo: Tran Lam Dong

Chapter 6

EFFECTS OF LIGHT AVAILABILITY ON CROWN STRUCTURE, BIOMASS PRODUCTION, LIGHT ABSORPTION AND LIGHT-USE EFFICIENCY OF *HOPEA ODORATA* ROXB. PLANTED IN GAPS IN A NURSE-CROP PLANTATION OF *ACACIA* HYBRID

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Abstract

Understanding how *Hopea odorata* alters its architectural traits and growth rate in response to changing light environments is essential when designing and manipulating mixed-species plantations containing this species. Seedlings of *H. odorata* were planted in 22-m circular gaps within a 3-yr-old *Acacia* hybrid plantation, and in 5 and 7.5 m strip gaps within a 2.5-yr-old *A.* hybrid plantation. Crown structure, absorption of photosynthetically active radiation (APAR) and whole-plant light-use efficiency (LUE; above-ground biomass growth or wood growth per unit APAR) of the seedlings over a gradient of light across the circular gap were examined for two years. Biomass production increased exponentially from the gap perimeter to the gap centre. This was largely due to an exponential increase in APAR and a minor increase in LUE. The large increase in APAR was associated with an increase in crown size (leaf area) and a reduction in shading from the nurse trees. Conversely, APAR per unit leaf area decreased towards the gap centre, probably due to steeper branch and leaf angles in order to avoid high radiation. The increase in LUE was probably due to increased photosynthesis rather than changes in biomass partitioning. In the strip-gap planting, the PAR was similar to that at the edge of the circular gaps; however the light pattern was dominated by sun flecks in the strip gap and direct sunlight in the circular gap. While the LUE of the more shaded *H. odorata* trees in the strip gaps was much higher, this was not enough to make up for the much lower APAR and hence biomass production. This study shows that *H. odorata* is able to grow under a wide range of PAR and that the availability of PAR has a strong influence on its growth. While the strip gaps used in this study appeared to be too narrow, the circular gap indicated that nurse plantings are an effective silvicultural design for establishing *H. odorata* provided that competition for other resources is managed.

Keywords: Dipterocarp, light absorption, MAESTRA, shade tolerant

6.1. Introduction

Growth and biomass production are strongly influenced by light absorption (APAR) and whole-plant light-use efficiency (LUE). Managing inter- and intra-specific competition and their effects on APAR and LUE are essential to the success of mixed-species plantations (le Maire *et al.*, 2013). Stratification of canopies is a strategy that enables mixed-species stands both to share and to absorb more light (Niinemets, 2010; le Maire *et al.*, 2013). If a nurse crop such as *Acacia* hybrid is sun-adapted and allows enough light to penetrate its canopy, a shade-adapted subdominant species, such as the dipterocarp *Hopea odorata*, may grow in the understorey and total stand APAR may be greater than that of monocultures of the sun-adapted species. Differences in leaf chemical traits enable shade-adapted species to assimilate more CO_2 per unit of light (Lee *et al.*, 1997), and this results in higher whole-plant LUE (Ashton *et al.*, 2006). However, in spite of their contrasting physiological and chemical properties, large differences in growth rate between *H. odorata* and *Acacia* hybrid have resulted in the suppression of *H. odorata* in the mixed-species plantations in Vietnam (Tam, 2007). It was shown in Chapter 5 that *H. odorata* requires, and can respond to, increasing levels of incident radiation with plant development. Examination of how crown structure, light absorption and LUE of *H. odorata* change with light availability should enable better design and management of these mixed-species plantations.

Crown size is positively correlated with the availability of light provided there is a sufficiency of other resources (Valladares and Niinemets, 2007). Plants also make

various adjustments to their crown architecture so that incident light can be harvested more efficiently (Niinemets, 2010). For example to maximise light interception, branch growth of shade plants is more lateral than that of sun plants (Chen *et al.*, 1996; King, 1998), and the leaves of shade-adapted plants are usually thinner in order to construct a greater leaf area for more light absorption for a given biomass investment in foliage (Niinemets, 2010). Leaves of dipterocarp species have been found to be thinner in the understorey and with larger palisade and spongy cells than in canopy gaps (Cao, 2000; Lee *et al.*, 2000). Leaves of shade-adapted plants also lean downward if exposed to high irradiation to avoid photo-damage (Watling *et al.*, 1997). These characteristics can be used to help interpret the effects of incident radiation on plant behaviour.

Plant biomass production is strongly related to light interception and LUE (Binkley *et al.*, 2010; Forrester *et al.*, 2013; le Maire *et al.*, 2013), and greater biomass production results from capturing more light and/or using light more efficiently (Binkley *et al.*, 2010). As long as a species is adapted to the ambient light environment, plant growth rate will tend to increase with APAR, its trajectory being determined by resource availability and any changes in LUE (Forrester *et al.*, 2013). In mixed-species plantations however, in spite of the stratified canopy offering the potential benefit of capturing more light, LUE may be compromised because of interspecific competition for those resources (le Maire *et al.*, 2013).

This paper examines how crown structure of *H. odorata* changes along a light gradient created in a circular gap within an *Acacia* hybrid plantation, and also within strip gaps that have a similar light availability to the border of the circular gap. The MAESTRA model is then used to explore the relationship between growth rate and light availability in the context of the absorption of light (APAR) and its efficiency of use

(LUE). The relevance of this information to the management of mixed-species plantations is discussed.

6.2. Materials and methods

Location, climate, soil and plantation establishment are as described in Chapter 5.

6.2.1. Experimental design

Sixteen-month old seedlings of *H. odorata* were planted in three 22-m diameter, circular gaps within a 10.5-m high, 3-yr-old *Acacia* hybrid plantation in September 2011 (see Table 5.2 in Chapter 5). The same gap selected for physiological measurements (see Chapter 5) was used for this experiment. Four treatments at four distances along a radial line from the gap perimeter (GP) to the gap centre viz -1 m (G-1), 3 m (G3), 6 m (G6) and 9 m (G9), were used to examine changes in crown structure, biomass production, light absorption and light-use efficiency of *H. odorata* seedlings with increasing distance from the GP.

A second trial approximately 0.5 km away was also planted in September 2011 using the same *H. odorata* seedlings, but in strip gaps of 5 m (SG5) and 7.5 m (SG7.5) width within a 9.1-m high, 2.5-yr-old *Acacia* hybrid plantation (see Table 6.5). Each treatment was replicated by three rows. Each row has 30 trees planted in every 2 m, and oriented in a NE-SW direction; the trial was used to measure the same variables as in the circular gap.

6.2.2. Measurements and sampling

6.2.2.1. Light

Transmitted photosynthetically active radiation (PAR) was measured in August 2012, one year after planting *H. odorata*. For circular gap, PAR measurement was described in Chapter 5. For strip gap, a randomly selected row in each treatment was used for PAR measurement. Seven quantum sensors (Delta-T Devices QS2 400 and 700 nm) were horizontally mounted at 1.5 m height above ground at every 3 m. The sensors were connected to a data logger (Campbell Scientific CR1000 through an AM416 multiplexer) between 21th August and 3rd September, 2012. PAR (μmol m^{-2} s^{-1}) was recorded automatically every 5 min as the average of data taken every 30 s; total incident PAR was similarly recorded from three quantum sensors located in an open area 0.5 km from the site. The PAR in each treatment was calculated as relative daily PAR (%).

Total annual PAR was measured from September 2012 to August 2013. Three quantum sensors were horizontally mounted in an open area 0.5 km from the experimental site. The sensors were connected to a data logger (CR800 - Campbell Scientific through an AM416 - Campbell Scientific multiplexer) and PAR (μmol m^{-2} s^{-1}) was recorded automatically every 30 min as the average of data taken every 30 s.

6.2.2.2. Growth, biomass and crown dimensions

Acacia hybrid

In August 2012 and August 2013, all acacia trees in the three rows around the circular gaps and each side of the strip gaps were measured for diameter at breast height ($D_{1.3A}$;

cm), total height (H_{tA}; m), crown length (L_{cA}; m), and crown diameter (D_{cA}; m). Their x and y coordinates were also recorded (Fig. 6.1).

In August 2012, seven representative trees based on $D_{1.3A}$ were randomly selected in the circular gap experiment for destructive sampling; the trees covered the range of $D_{1.3A}$ from the smallest to largest classes (Appendix 6.1), and were at least 15 m from the GP to avoid any disturbance to the acacia canopy around and close to the gap edge. Each tree was felled and measured for H_{tA} and L_{cA}; L_{cA} was defined as the distance between the top of the crown to the point of insertion of the lowest live branch.

The L_{cA} of each tree was divided into two zones of equal length. In each zone, the diameter of all branches at 40 mm from the stem and their height of emergence were measured. A subsample of five branches representing the range of branch diameters was selected from each zone. Each sample branch was measured for total length (L_{bA}; mm), green branch length (length of branch with leaves; L_{gbA}; m), angle from stem (θ_{bA}; ^{o}), and the horizontal angle of three representative leaves (θ_{lA}; ^{o}), one each at the branch tip, middle and branch base. Fresh branch wood and leaves of each sample branch were weighed separately. A representative subsample of branch wood was weighed fresh and then dried to constant weight at 65^{o}C, cooled over a desiccant and weighed. A representative subsample of 20 leaves representing the range of leaf sizes and ages was also weighed fresh, scanned for measurement of leaf area (LA) using Fiji software (Schindelin *et al.*, 2012), and then dried to constant weight at 65^{o}C, cooled over a desiccant and weighed. The LA to leaf dry weight ratio was used to calculate the specific leaf area (SLA) (cm^2 g^{-1}) for each branch. Subsample values were used to calculate total branch and leaf dry mass, and SLA for the total LA of each branch.

Each stem was measured for diameter over- and under-bark at 0.1 m, 1.3 m, crown base, and at the junction of the crown zones. The whole stem was weighed fresh. Five-cm thick stem disks were collected from the points where stem diameters were measured. Under- and over-bark fresh weight and volume were determined by weighing and by water displacement, respectively. Dry weight of each disk was determined after drying to constant weight at 65^{o}C. Wood density (g cm^{-3}) of each disk was based on the mean dry weight and volume of the disk. Wood mass (Mg) was determined from the density and volume of each log length, where density was the mean value of the disks at either end of each log and volume was calculated as a frustrum based on diameters at either end of each log and log length.

Seven representative trees at least 15 m from the gap edge were also randomly selected in the strip gap trial for destructive sampling. Sampling and measurement methods were as in the circular gap experiment, but the L_{cA} of each tree was divided into three zones of equal length.

Hopea odorata

The x- and y-coordinates of all trees in the gap were measured (Fig. 6.1).

Non-destructive measurements of crown structure and biomass were conducted in the same gap at age 1 yr. The same three trees (one mean tree, one of +1 standard deviation (SD) and one of –1 SD, based on $D_{0.3H}$ and H_{tH}; see Chapter 5) selected for measurements of SLA were used for sampling (Appendix 6.1). The canopy of each sample tree was divided into upper and lower zones of equal length; live branches were present to ground level. In each zone, the number of branches ($\#_{bH}$) was recorded, and

all branches were measured for diameter at 4 cm from the stem, total branch length (L_{bH}), and length of branch with green leaves (L_{gbH}). Five sample branches representing the range of branch diameters were selected in each zone for measurement of leaf area (LA), leaf angle (θ_{llH} and θ_{luH}; ^{o}) and branch angle of the lower and upper crown zones (θ_{blH} and θ_{buH}; ^{o}), respectively. For each branch, a digital picture was taken of all leaves while held in a 40 × 30 cm (1,200 cm^2) glass folder with white colour background. Leaf area of each sample branch was determined using CAN-EYE V6.3.3 software after correction for barrel distortion by Photoshop CS3 (Adobe) software. Leaf angles of three representative leaves from the five sample branches in each crown zone were measured from the horizontal; time of measurement was between 08:30 – 16:00 h and the sample trees were randomly selected.

Similarly, the same trees selected for SLA sampling at age 2 yrs (see Chapter 5) were destructively harvested for biomass and crown structure analysis. For estimation of biomass at age 1 yr, the five sample branches selected in each crown zone representing the range of branch sizes overlapped with those sampled at age 1 yr. Measurements were done as in the Year 1 sampling. Leaves of each sample branch were scanned (Canon Scanner Lide 210). The remaining leaves, the branches and stem in each crown zone were weighed fresh. All sample branches and five 10-cm length sections equally distributed over the stem length were collected and dried to constant weight at 65^{o}C for calculation of dry stem weight. A root ball containing all the roots and defined by a radius 0.5 m from the stem and 0.6 m depth was excavated manually; roots were separated into five depth levels: 0 – 10, 10 – 20, 20 – 30, 30 – 50 and >50 cm, and three root sizes: <2, 2 – 5 and >5 mm, weighed fresh, and then were dried to constant weight at 65^{o}C separately to estimate dry root weight.

In the strip gap trial, three sample trees in each treatment, one mean tree, one of +1 SD and one of –1 SD, based on $D_{0.3H}$ and H_{tH} were selected for sampling. The same sampling processes and data measurement as in the circular gap experiment were used.

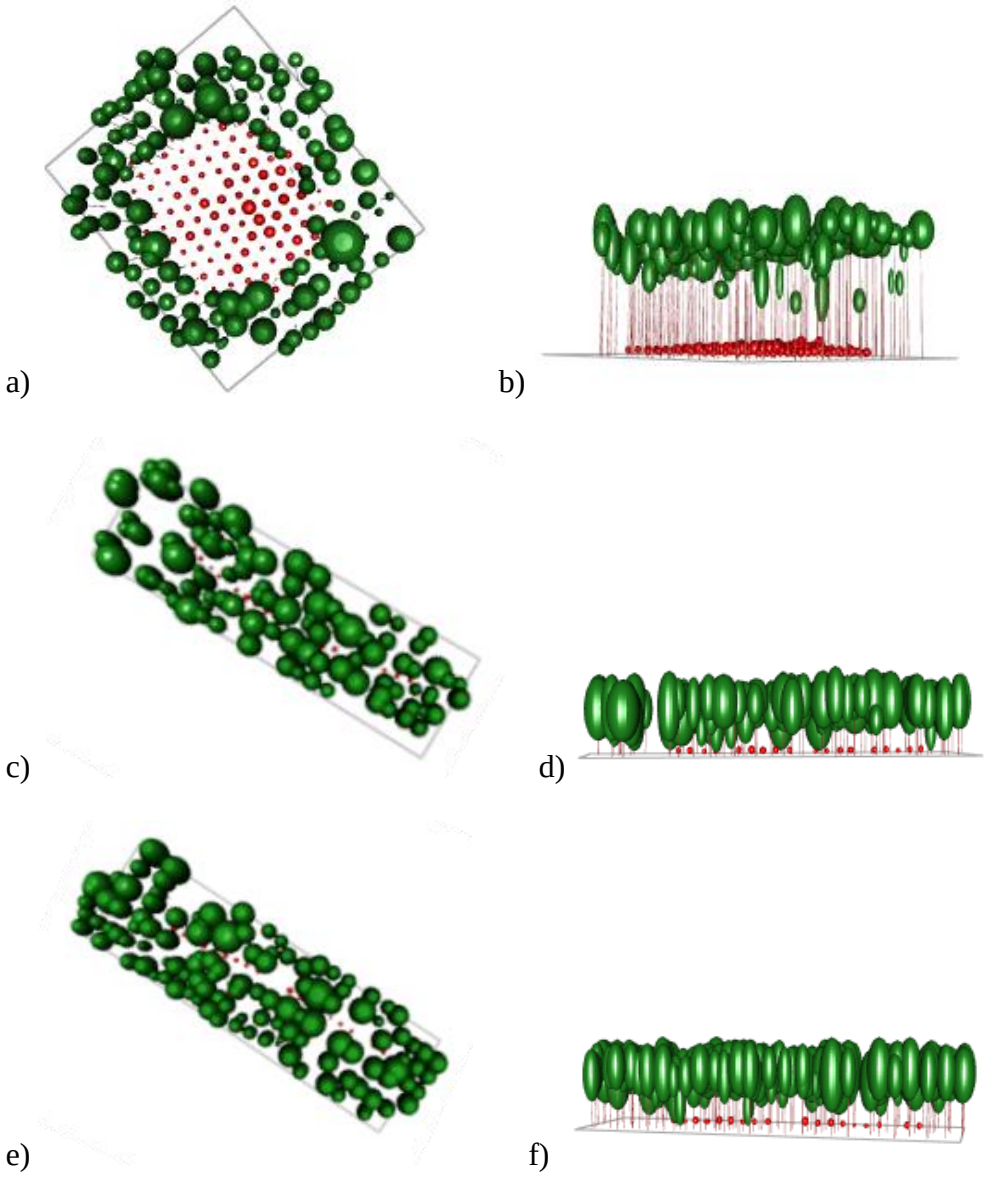

Figure 6.1 Representations of the circular (a, b) and strip gaps (SG5: c and d; SG7.5: e and f) in plan view (a, c and d) and vertical section (b, d and f) of the *Hopea odorata* (in red) at age 1 yr (August 2012) within the *Acacia* hybrid nurse crops (in green). The sizes of the symbols represent the diameters (plan view) and heights (vertical section) of the trees. This information was used as inputs for the MAESTRA model

6.2.3. Calculation

6.2.3.1. Biomass and crown dimensions

For *Acacia* hybrid in both experiments, allometric equations between branch basal area (BA_{bA}) and dry branch weight (W_{bA}), BA_{bA} and dry leaf weight (W_{lA}), and BA_{bA} and LA were developed based on the destructive sampling in 2012 (Appendix 6.2). These equations were used to estimate W_{bA}, W_{lA} and LA of each sample tree. Allometric equations between $D_{1.3A}$ and W_{bA}, W_{lA}, LA, and dry stem weight (W_{sA}) were then developed to estimate these variables for all measured trees around the gaps.

For 1-yr-old *H. odorata* trees in the circular gap experiment, non-destructive data of all 1-yr-old sampled trees were used to develop allometric equations for each crown zone between BA_{bH} and LA after testing for homogeneity of the variances between treatments (Appendix 6.3). Leaf weight (W_{lH}) was estimated from LA and SLA in the different crown zones of each sampled tree. Destructive data from the 2-yr-old sampled trees were used to develop allometric equations for each crown zone between BA_{bH} and W_{bH}, and $D_{0.3H}$ and H_{tH} and W_{sH} after testing for homogeneity of the variances between treatments, and used to estimate branch and stem weight of the 1-yr-old trees.

For 2-yr-old *H. odorata* trees, destructive data of all 2-yr-old sampled trees were used to develop allometric equations for each crown zone between $D_{0.3H}$ and W_{bH}, W_{lH}, LA, and W_{sH} after testing for homogeneity of the variances between treatments. Calculations were done in the same way for *H. odorata* trees in the strip gap experiment.

The distribution of LA in the crown zone for both *A.* hybrid and *H. odorata* trees was calculated following Medhurst and Beadle (2001). The proportion of a branch with

leaves from a given branch that originated in one crown zone but distributed in the next (upper) crown zone (l_{BU}) was estimated as: $l_{BU} = h_{BT} - h_{CP}$

where h_{BT} is the height at each branch tip: $h_{BT} = h_0 + \cos\theta * l_B$

where h_0 is height of branch emergence and l_B is branch length; h_{CP} is height that separates the two crown zones. The allometric equations of the crown zone in which the major proportion of l_{BU} (>50%) was located was used to estimate the leaf area and leaf weight of that branch.

Allocation of biomass (Hunt, 2003) was calculated for age 1 and 2 yrs, including total plant mass (leaf + stem + branch + root mass; g), leaf mass ratio (leaf mass/total plant mass; g g^{-1}), stem mass ratio (stem + branch + petiole mass/total plant mass; g g^{-1}), and root mass ratio (root mass/total plant mass; g g^{-1}).

The leaf area density (LAD; m^2 m^{-3}) of each crown zone was determined as leaf area (m^2) per unit volume of the crown zone (m^3). Crown volume was calculated based on crown radius and zone length assuming that the upper and lower zones were a half ellipse for both species (Forrester *et al.*, 2012, 2013).

6.2.3.2. Absorption of photosynthetically active radiation (APAR)

The absorption of PAR by individual tree crowns was estimated using the MAESTRA model (Wang and Jarvis, 1990; Medlyn, 1998; Forrester *et al.*, 2013; le Maire *et al.*, 2013). The crown shape of individual trees for both species was defined as a half-ellipse. Shading from neighbouring trees was determined by specifying the position of each tree in the stand using the x- and y-coordinates (Fig. 6.1). Shading of acacia nurse trees was

determined by specifying position and dimension of all measured trees in the three rows from the gap perimeter (Fig. 6.1). A buffer area was extended a further 15 m from the third row; the position and dimension of these buffer trees were respectively the mean space occupied and dimensions of the measured trees. Leaf transmittance and leaf and soil reflectance values for *Acacia mangium* and *Eucalyptus grandis* (le Maire *et al.*, 2013) were used for *A.* hybrid and for *H. odorata*, respectively (Appendix 6.4).

APAR (GJ $tree^{-1}$ and GJ m^{-2}) was calculated for each crown based on the average PAR measured every 30 min for the period September 2012 to August 2013 and crown structure parameters. Light-use efficiency (LUE; g MJ^{-1}) was calculated as above-ground biomass (AGB-LUE) and wood (the stem and branch biomass; Wood-LUE) growth per unit APAR (Forrester *et al.*, 2013) for the same period.

6.2.4. Statistical analysis

SPSS version 21 was used for all statistical analyses. Levene's test was used to examine the homogeneity of variances between treatments. One-way ANOVA was used to compare means of crown structure parameters (L_{cH}, $\#_{bH}$, θ_{blH}, θ_{buH}, LA, LAD and θ_{lH}), AGB and wood growth, APAR, AGB-LUE, and Wood-LUE at the 0.05 level. Tukey adjustment for multiple comparisons was used to determine significant differences among treatments. Independent-sample t-tests were used to compare means of crown-structure parameters between the lower- and upper-crown zones. Relationships between BA_b and biomass parameters, and stem diameter and biomass parameters were examined by non-linear regression. Relationship between APAR and AGB, APAR and wood growth, and APAR and leaf area were examined by generalized linear regression.

Relationships between distance from gap perimeter and APAR, AGB and wood growth were examined by non-linear regression.

6.3. Results

6.3.1. Growth of *A.* hybrid

For the circular gap, tree growth variables were described in Table 5.2 of Chapter 5. In 2012, stand W_{bA} was 4.06 Mg ha^{-1}, W_{lA} was 4.22 Mg ha^{-1}, dry over- and under-bark stem weight (W_{soA} and W_{suA}) were 59.4 and 50.5 Mg ha^{-1}, and fresh over-bark stem weight (W_{sfA}) was 139.9 Mg ha^{-1}; LA was 46,555 m^2 ha^{-1}, equivalent to a leaf area index of 4.7 (Appendix 6.5).

For the strip gap, stocking density of the *Acacia* hybrid at planting of *H. odorata* in September 2011 was 1,088 trees ha^{-1}; mean $D_{1.3A}$ was 7.5 cm, H_{tA} was 9.1 m, L_{cA} was 6.2 m and D_{cA} was 2.5 m (Appendix 6.5). In August 2012 and August 2013, $D_{1.3A}$ was 10.9 and 12.9 cm, H_{tA} was 13.5 and 17.5 m, L_{cA} was 9.0 and 10.1 m and D_{cA} was 2.5 and 3.5, respectively. In 2012, stand W_{bA} was 6.93 Mg ha^{-1}, W_{lA} was 4.66 Mg ha^{-1}, W_{soA} was 38.4 Mg ha^{-1}, W_{suA} was 32.6 Mg ha^{-1} and W_{sfA} was, , 72.3 Mg ha^{-1}; LA was 50,098 m^2 ha^{-1} (LAI = 5.0) (Appendix 6.5).

6.3.2. Crown structure of *H. odorata*

In the circular gap at age 1 yr (August 2012), treatment affected L_{cH}, $\#_{bH}$, θ_{blH}, LA, θ_{llH}, and θ_{luH}, but not θ_{buH} and LAD (Table 6.1a). Crown length and LA increased significantly from the G-1 to the G6 treatment, but were not significantly different between G6 and G9. The number of live branches in the G-1 and G3 treatments was significantly smaller than in the G6 and G9 treatments. Leaf angles in both the lower

and upper crown zones of the G9 treatment were significantly higher than for other treatments. Branch angle of the lower crown zone of the G9 treatment was significantly higher than for other treatments. Crown zone had significant effects on θ_{bH} and θ_{lH}. While θ_{buH} was significantly higher than θ_{blH} in the G-1 treatment, it was lower in the G9 treatment. Leaf angles of the upper crown zone were significantly higher than those of lower crown zone in the G6 and G9 treatments.

At age 2 yrs, treatment affected L_{cH}, $\#_{bH}$, θ_{blH}, θ_{buH}, and LA, but not LAD (θ_{lH} was not measured in age 2 yrs) (Table 6.1a). Crown length and LA increased significantly from G-1 to G9. The number of live branches was only significantly different between G-1 and G9. While θ_{buH} in the G-1 treatment was significantly higher than θ_{blH}, it was significantly lower than in the G6 treatment.

In strip gap, there were no treatment effects on crown structure parameters in both years (Table 6.1b).

Table 6.1a Crown structure: Crown length (L_{cH}), number of live branches per tree ($\#_{bH}$), branch angle (θ_{bH}), total leaf area (LA), leaf area density (LAD) and leaf angle (θ_{lH}) of *Hopea odorata* planted in a 22-m diameter gap within a 3-yr-old *Acacia* hybrid plantation (means ± 1 SD)

Parameters	Details	1 yr-old				2 yr-old			
		G-1	G3	G6	G9	G-1	G3	G6	G9
L_{cH} (m)	n	149	109	69	29	138	105	69	29
	Mean ± SD	0.89 ± 0.16 a	1.08 ± 0.26 b	1.33 ± 0.25 c	1.37 ± 0.25 c	1.07 ± 0.26 a	1.44 ± 0.37 b	1.98 ± 0.33 c	2.17 ± 0.36 d
$\#_{bH}$	n = 3	16.3 ± 1.7 a	19.3 ± 3.1 a	32.0 ± 4.0 b	36.3 ± 1.5 b	21.0 ± 10.8 a	26.0 ± 5.3 ab	37.3 ± 5.1 ab	40.7 ± 6.5 b
θ_{bH} (^{o}) (n = 15)	LZ	56.8 ±14.2 a	60.0 ± 9.3 a	61.0 ± 7.4 a	70.0 ± 6.1 b*	60.7 ± 10.7 a	65.7 ± 8.4 ab	69.7 ± 11.2 b*	66.1 ± 9.3 ab
	UZ	65.5 ± 8.7 *	65.7 ± 8.2	65.5 ± 6.0	61.0 ± 6.2	70.3 ± 11.3 a*	68.5 ± 10.6 ab	63.0 ± 15.0 b	63.2 ± 9.1 b
LA (m^2)	n = 3	0.24 ± 0.1 a	0.46 ± 0.22 b	0.75 ± 0.31 c	0.74 ± 0.23 c	0.48 ± 0.43 a	0.71 ± 0.26 b	2.15 ± 1.1 c*	2.39 ± 1.24 c*
LAD (m^2 m^{-3})	n	55	38	22	10	55	37	22	10
	Mean ± SD	0.51 ± 0.16	0.55 ± 0.18	0.48 ± 0.12	0.43 ± 0.13	0.47 ± 0.19	0.42 ± 0.12	0.39 ± 0.07	0.45 ± 0.11
θ_{lH} (^{o}) (n = 15)	LZ	35.7 ± 16.3 a	37.7 ± 10.8 a	30.0 ± 14.6 a	53.7 ± 9.9.0 b				
	UZ	40.2 ± 18.7 a	36.1 ± 12.4 a	42.7 ± 8.1 a*	73.0 ± 11.0 b*				

ANOVA with Tukey adjustment was used for multiple comparisons. Within a row at each age, the treatments, G-1, G3, G6 and G9 (-1, 3, 6 and 9 m from gap perimeter, respectively), with a similar letter are not significantly different at the 0.05 level. * indicated a significant higher of mean between crown zones compared by T-test; LZ: Lower crown zone, UZ: Upper crown zone

Table 6.1b Crown structure: crown length (L_{cH}), number of live branches per tree ($\#_{bH}$), branch angle (θ_{bH}), total leaf area (LA), leaf area density (LAD) and leaf angle (θ_{lH}) of *Hopea odorata* planted in 5 and 7.5 m strip gaps within a 2.5-yr-old *Acacia* hybrid plantation (means ± 1 SD)

Parameters	Details	1 yr-old		2 yr-old	
		SG5	SG7.5	SG5	SG7.5
L_{cH} (m)	n	18	19	18	19
	Mean ± SD	1.13 ± 0.17	1.20 ± 0.08	1.54 ± 0.32	1.72 ± 0.29
$\#_{bH}$	n = 3	16.2 ± 3.1	19.2 ± 3.8	20.5 ± 4.3	30.2 ± 5.0
θ_{bH} (^{o}) (n = 15)	LZ	55.7 ± 9.9	58.6 ± 10.8	64.4 ± 9.5	69.1 ± 9.7
	UZ	62.3 ± 9.4	62.7 ± 8.5	75.6 ± 9.7	72.3 ± 7.8
LA (m^2)	n = 3	0.37 ± 0.11	0.43 ± 0.11	0.80	1.26
LAD (m^2 m^{-3})	n	18	19	18	19
	Mean ± SD	0.38 ± 0.14	0.46 ± 0.33	0.30 ± 0.06	0.33 ± 0.12
θ_{lH} (^{o}) (n = 15)	LZ	33.6 ± 19.2	27.4 ± 17.0		
	UZ	27.6 ± 14.8	22.5 ± 17.1		

ANOVA with Tukey adjustment was used for multiple comparisons. Within a row of an age, the treatments, G-1, G3, G6 and G9 (-1, 3, 6 and 9 m from gap perimeter, respectively), with a similar letter are not significantly different at the 0.05 level. * indicated a significant higher of mean between crown zones compared by T-test; LZ: Lower crown zone, UZ: Upper crown zone

6.3.3. Biomass and leaf area of *H. odorata*

At age 1 yr, the annual increment of total biomass, as well as leaf, stem and root mass of the mean tree increased significantly from the G-1 to the G6 treatment, but were not different between G6 and G9 (Table 6.2). At age 2 yrs, total and leaf biomass increased significantly from G-1 to G6; stem and root mass were significantly different between

each of G-1, G3 and G6, but not G6 and G9. The annual increments of the total, leaf, stem and branch, and root biomass were significantly higher in the second than first year in the G6 and G9 treatments; root mass at G-1 was significantly higher in the first than second year. Leaf, branch and stem, and root mass ratios were not significantly different between treatments at both ages 1 and 2 yrs.

Annual increment of leaf area in years 1 and 2 increased significantly from the G-1 to G6 treatments, but was not different between G6 and G9 (Table 6.2). The increments of leaf area of the G6 and G9 treatments in the second year were significantly higher than that in the first year.

Annual AGB and wood growth of 2-yr-old trees increased significantly from gap perimeter to gap centre, and were best described by a quadratic equation (Fig. 6.2b and 6.2c); at G9 they were about two-, 3.5- and 9-fold higher than in the G6, G3, and G-1 treatments, respectively (Table 6.3a).

Table 6.2 Annual biomass and leaf area increment (age 1 and 2 yrs) of *Hopea odorata* planted in a 22-m diameter gap within a 3-yr-old *Acacia* hybrid plantation (means ± 1 SD; n = 3 for each treatment)

Treatment	1 yr-old				2 yr-old			
	G-1	G3	G6	G9	G-1	G3	G6	G9
Leaf (g tree^{-1})	13.8 ± 6.6 a	31.2 ± 16.8 b	55.4 ± 24.7 c	54.3 ± 17.6 c	18.1 ± 16.7 a	24.7 ± 8.5 b	122.6 ± 63.3 c*	150.5 ± 79.1 d*
Stem and branch (g tree^{-1})	39.1 ± 14.7 a	73.1 ± 32.4 b	118.0 ± 45.0 c	115.6 ± 33.1 c	46.4 ± 24.5 a	108.9 ± 55.2 b	301.2 ± 122.7 c*	452.0 ± 216.3 c*
Root (g tree^{-1})	33.2 ± 10.3 a*	54.7 ± 19.4 b	81.2 ± 24.3 c	79.2 ± 19.1 c	23.4 ± 14.5 a	48.6 ± 30.1 b	199.1 ± 69.9 c*	240.4 ± 64.2 c*
Total mass(g tree^{-1})	86.1 ± 31.6 a	159.0 ± 68.6 b	254.6 ± 94.0 c	249.1 ± 69.8 c	87.9 ± 55.8 a	182.2 ± 93.4 b	622.9 ± 256.5 c*	842.9 ± 358.9 d*
Leaf area increment (m^2 tree^{-1})	0.16 ± 0.10 a	0.38 ± 0.22 b	0.67 ± 0.31 c	0.66 ± 0.23 c	0.24 ± 0.21 a	0.25 ± 0.09 a	1.40 ± 0.72 b*	1.66 ± 0.86 b*
Leaf mass ratio	0.19 ± 0.02	0.21 ± 0.02	0.23 ± 0.03	0.23 ± 0.02	0.17 ± 0.06	0.19 ± 0.05	0.20 ± 0.02	0.18 ± 0.03
Stem and branch mass ratio	0.45 ± 0.03	0.46 ± 0.04	0.46 ± 0.05	0.46 ± 0.04	0.51 ± 0.06	0.53 ± 0.02	0.48 ± 0.03	0.51 ± 0.04
Root mass ratio	0.36 ± 0.02	0.33 ± 0.02	0.31 ± 0.03	0.31 ± 0.03	0.32 ± 0.02	0.28 ± 0.06	0.32 ± 0.02	0.31 ± 0.06

ANOVA with Tukey adjustment was used for multiple comparisons. Within a row for each age, the treatments, G-1, G3, G6 and G9 (-1, 3, 6 and 9 m from gap perimeter, respectively), with a similar letter are not significantly different at the 0.05 level. * indicates a significantly higher mean of each growth parameter between age 1 and 2 yrs

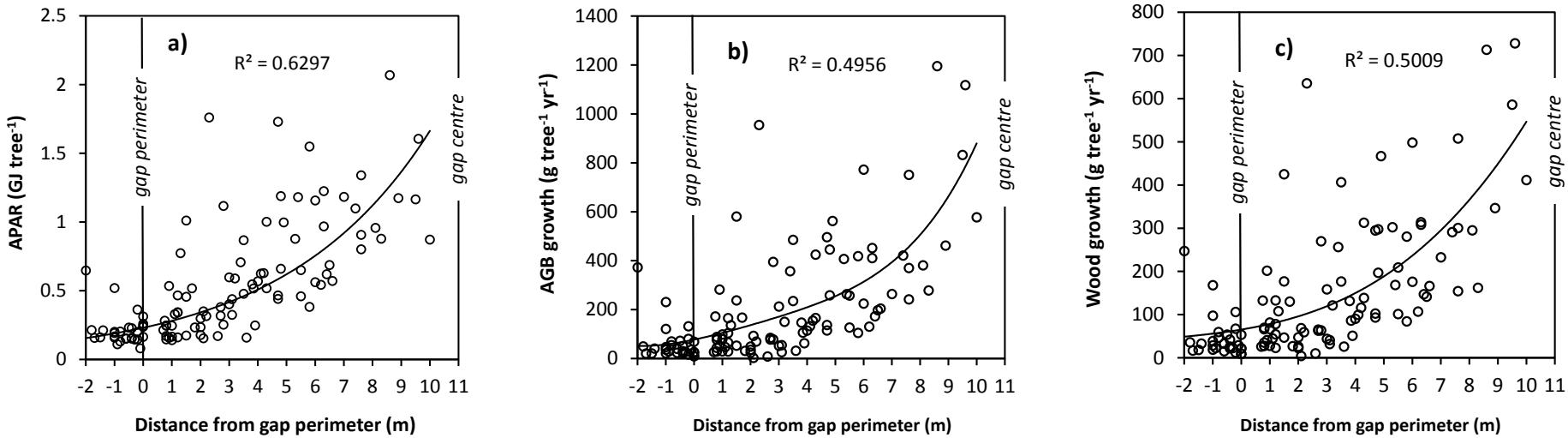

Figure 6.2 Absorbed photosynthetically active radiation (APAR) (a), above-ground biomass (AGB; b) and wood growth (c) of *Hopea odorata* between age 1 and 2 yrs planted in a 22-m diameter gap within a 3-yr-old *Acacia* hybrid plantation as a function of distance from the gap perimeter; ° observation, — mean fitted by exponential (APAR) and quadratic (AGB and wood growth) equations

6.3.4. Light interception and LUE

In circular gap, APAR (GJ tree^{-1} yr^{-1}) increased exponentially from the gap perimeter to the gap centre (Fig. 6.2a); it was about 1.5-, 2.5- and 5-fold higher in the G9 than G6, G3, and G-1 treatments, respectively (Table 6.3a). Conversely, the absorption per leaf area of G9 was significantly lower than G3 and G-1, 0.61 *v.* 0.75 – 0.76 (GJ m^{-2} yr^{-1}), and was not different between the other treatments. Light-use efficiency was significantly greater in the G9 than other treatments. Trees at G9 produced 0.50 g MJ^{-1} AGB and 0.35 g MJ^{-1} wood *v.* 0.28 – 0.35 g MJ^{-1} and 0.22 – 0.26 g MJ^{-1} in the other treatments, respectively (Table 6.3a). APAR (GJ tree^{-1} yr^{-1}) was strongly related to tree leaf area (Fig. 6.3). However there were no significant differences between treatments.

In strip gaps, there was no significant difference in PAR, AGB and wood growth, APAR per tree, AGB-LUE and Wood-LUE between treatments, except for APAR per unit leaf area (Table 6.3b).

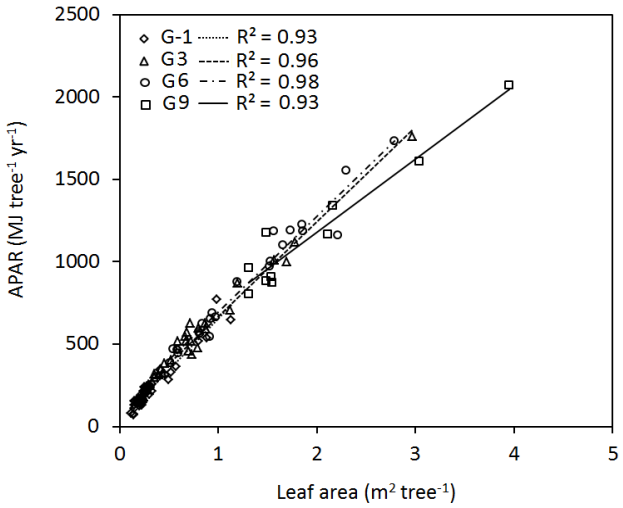

Figure 6.3 Relationship between leaf area and absorbed photosynthetically active radiation (APAR) of *Hopea odorata* planted in a 22-m diameter gap within a 3-yr-old *Acacia* hybrid plantation. Treatments, G-1, G3, G6 and G9, were -1 m, 3 m, 6 m and 9 m from gap perimeter to gap centre

Table 6.3a Absorbed photosynthetically active radiation (APAR) and light-use efficiency (AGB-LUE) of *Hopea odorata* planted in a 22-m diameter gap within a 3-yr-old *Acacia* hybrid plantation (means ± 1 SD)

Treatment	G-1	G3	G6	G9
n	54	34	22	10
PAR (%)	24.2 ± 6.4 a	45.4 ± 7.2 bc	55.6 ± 4.2 cd	59.1 ± 1.7 d
AGB growth (g tree^{-1} yr^{-1})	69.9 ± 68.6 a	172.4 ± 199.6 b	311.1 ± 173.2 c	620.9 ± 341.1 d
Wood growth (g tree^{-1} yr^{-1})	55.3 ± 48.3 a	130.4 ± 139.1 b	226.5 ± 114.6 c	420.6 ± 207.8 d
APAR (GJ tree^{-1} yr^{-1})	0.23 ± 0.14 a	0.50 ± 0.34 b	0.87 ± 0.38 c	1.18 ± 0.40 d
APAR (GJ m^{-2} yr^{-1})	0.75 ± 0.12 a	0.76 ± 0.10 a	0.69 ± 0.07 ab	0.61 ± 0.09 b
AGB-LUE (g MJ^{-1} yr^{-1})	0.30 ± 0.20 a	0.28 ± 0.15 a	0.35 ± 0.11 ab	0.50 ± 0.16 b
Wood-LUE (g MJ^{-1} yr^{-1})	0.25 ± 0.16 ab	0.22 ± 0.11 a	0.26 ± 0.08 ab	0.35 ± 0.11 b

ANOVA with Tukey adjustment was used for multiple comparisons. Within a row the treatments, G-1, G3, G6 and G9 (-1, 3, 6 and 9 m from gap perimeter, respectively), with a similar letter are not significantly different at the 0.05 level

Table 6.3b Absorbed photosynthetically active radiation (APAR) and light-use efficiency (AGB-LUE) of *Hopea odorata* planted in 5-m and 7.5-m strip gaps within a 2.5-yr-old *Acacia* hybrid plantation (means ± 1 SD)

Treatment	SG5	SG7.5
n	18	19
PAR (%)	19.3 ± 3.6	20.2 ± 5.0
AGB growth (g tree^{-1} yr^{-1})	200.2 ± 89.2	213.6 ± 99.9
Wood growth (g tree^{-1} yr^{-1})	141.3 ± 58.1	151.2 ± 64.0
APAR (GJ tree^{-1} yr^{-1})	0.23 ± 0.08	0.25 ± 0.06
APAR (GJ m^{-2} yr^{-1})	0.30 ± 0.07 a	0.35 ± 0.06 b
AGB-LUE (g MJ^{-1} yr^{-1})	0.90 ± 0.31	0.86 ± 0.36
Wood-LUE (g MJ^{-1} yr^{-1})	0.64 ± 0.21	0.61 ± 0.23

ANOVA with Tukey adjustment was used for multiple comparisons. Within a row, the treatments, SG5 and SG7.5 (gap widths of 5 and 7.5 m, respectively), with a similar letter are not significantly different at the 0.05 level

6.4. Discussion

6.4.1. Growth of *A.* hybrid nurse crop

At the stand level, the leaf area indices (LAI) of *Acacia* hybrid were similar between the two experiments. However, the number of *A.* hybrid trees ha^{-1} in the circular-gap experiment was about double that in the strip-gap experiment, and the crown lengths and widths of individual trees were less in the circular gap experiment. This restriction of crown development was probably caused by the higher stem density in the circular-gap experiment resulting in greater intra-specific competition for all resources (Eyles *et al.*, 2009). This capacity to manipulate the crown characteristics through stand density without having an influence of LAI may be useful in the management of the nurse crop and its interaction with the target crop.

Total biomass production of the *Acacia* hybrid was lower in the strip-gap experiment, indicating that light absorption and photosynthetic rate may have been different between the two experiments. As the crown length of individual trees in the strip-gap experiment was about double of that in the circular-gap experiment, a larger proportion of leaves in the canopy may have received lower incident levels of light than in the circular-gap experiment which resulted in lower canopy photosynthesis. In similarly large canopies of *Eucalyptus globulus*, O'Grady *et al.* (2008) observed that photosynthetic rate varied from 3 μmol m^{-2} s^{-1} in the lower canopy to 18 μmol m^{-2} s^{-1} in the upper canopy. However the larger crowns in the strip gaps probably contributed to the creation of the more shaded environment than experienced by the G-1 treatment in the circular gap which received similar levels of incident PAR. This suggests that closer

spacing in the nurse crop can be used to reduce the speed at which the nurse crop reoccupies the gap, possibly allowing greater development of the *H. odorata*.

Acacia hybrid is a fast growing species (Dong *et al.*, 2014). In both experiments, mean height when the *H. odorata* was planted was 7.5 to 9 m and the trees grew a further 7 m during the two years of the experiment. Such rapid development results in a potential pool of nutrient resources through litter production and turnover (Dong *et al.*, 2014). In both experiments, two years after the gaps created, the crowns of trees at the gap perimeter had developed substantial amounts of new crown into the gaps. Use of *A.* hybrid as a nurse crop will require regular manipulation to provide sufficient light for understorey trees in nurse-crop systems.

6.4.2. Effects of light availability on crown structure of *H. odorata*

Crown size is positively correlated with growth rate (Beadle, 1997) because it increases APAR, and in this study, crown diameter (Chapter 5), crown length, and the number of live branches of *H. odorata* were strongly and positively related to the increasing amounts of available PAR from the gap perimeter towards the gap centre.

Leaf angle was more vertical towards the centre of the gap, which is probably related to the need to avoid photoinhibition and heat-related stress (Watling *et al.*, 1997) due to the high light intensities near the gap centre. The same mechanism may have led to the higher leaf angles in the upper crown zone compared with the lower crown zone. Irradiation intensity also affected branch angle. In the upper crown zone at age 2 yrs, branches were more horizontal near the gap perimeter than at the gap centre; in the

lower crown zone at both ages, branches were more vertical. Shade-tolerant species adapt to the low light conditions by favouring lateral rather than vertical growth (Chen *et al.*, 1996; King, 1998) in order to maximise light absorption (Medhurst and Beadle, 2001). The more horizontal structure in the upper than lower crown zone at the gap perimeter indicated an effect of light on branching when *H. odorata* trees are adapted to low-light conditions. These findings confirm that *H. odorata* has plasticity in both leaf display and branching structure in response to light environment.

There were only minor and insignificant changes in leaf area density, suggesting that the most plastic crown architectural characteristics in *H. odorata* are crown length, width and leaf area, and to a lesser extent the leaf and branch angle. The less plastic nature of leaf area density has been found also for other species (Binkley *et al.*, 2010; Forrester *et al.*, 2012).

6.4.3. Biomass production in relation to light interception and LUE

The substantial increase in annual biomass increment of *H. odorata* trees from the gap perimeter to the gap centre was correlated with an increase in PAR. As for diameter and height growth (Chapter 5), this was related to decreasing interspecific competition for light and to some extent in the dry season, soil water. Higher biomass production results from either more light interception or higher light-use efficiency (Binkley *et al.*, 2010; Binkley, 2012). The significant increase of leaf area per tree from G-1 to G9 was positively correlated with an increase of APAR per tree. Trees at the gap centre captured five times more PAR and produced nearly 10× more biomass than those at the gap perimeter, indicating a strongly positive relationship between biomass production

and light interception (Beadle, 1997; Binkley *et al.*, 2013; Campoe *et al.*, 2013; Gspaltl *et al.*, 2013). On the other hand for a given leaf area, trees towards the gap centre had lower APAR (Table 6.3a), which was probably related to their steeper branch and leaf angles.

However, trees at the gap centre also had higher LUE, which is often associated with increasing light interception (Binkley *et al.*, 2010; Binkley, 2012). A greater LUE indicates either higher rates of photosynthesis and/or partitioning of C to wood production (Ryan *et al.*, 2010). In this circular gap, A_{max} of trees at the gap centre was significantly higher than at the gap perimeter (see Chapter 5). Plants adapted to high light environments in their native habitat tend to have a high photosynthetic rate at saturating light intensities, but in a low light environment, their LUE is lower than that of shade plants (Boardman, 1977; Givnish, 1988). Trees at the gap centre appeared to be adapted to the high light environment (Chapter 5) and intercepted more light, hence the higher LUE. However, partitioning of C to wood production was not different between treatments. Biomass allocation is affected by the availability of growth resources such as soil water (Eyles *et al.*, 2009). The low leaf water potentials found in G-1 and G3 treatments at the end of the dry season appear not to have affected the partitioning of biomass.

Although the levels of incident PAR in the G-1 treatment of the circular gap was similar to that of both treatments in the strip gap, the amount of AGB produced and the AGB-LUE were much lower in the circular gap (Table 6.3a and 6.3b). As the strip gaps were aligned NE-SW and their width was ≤7.5 m, the period of time of exposure to direct sunlight was shorter than in the circular gap. In addition, the gap was nearly closed after 2 yrs. The frequency distribution of 5-min averages of PAR in the strip gap

at age 1 yr was very different from that in the circular gap (Fig. 6.4; Fig. 5.3 in Chapter 5); in the strip gap, the proportion of intensities <50 μmol m^{-2} s^{-1} was much higher and >500 μmol m^{-2} s^{-1} was much lower. Therefore, *H. odorata* trees in the strip gap would have been more shade-adapted. Their higher AGB-LUE suggests that these trees had higher rates of photosynthesis than the G-1 trees in the circular gap, as their much lower APAR (GJ m^{-2}) produced a much higher AGB in the strip gap (Table 6.3b).

Canopy development is constrained by the availability of water and nutrients (Beadle, 1997). The potential capacity for higher biomass production of a multi-storey mixed-species plantation because of higher light absorption than in a monoculture may not be realised if growth resources are limiting (le Maire *et al.*, 2013; Forrester, 2014). In the circular gap trial, water competition between the *H. odorata* trees within 3 m of the gap perimeter and the *A.* hybrid trees was recorded at the end of the dry season (Chapter 5) and may have affected the growth of the *H. odorata*. Thus, the lower biomass growth of the G-1 and G3 treatments may have been partly affected by water competition. Such factors may have implications for the types of sites where such nurse-crop systems can be used; the slope of the relationships between growth and APAR or LUE might be lower on drier or less fertile sites where growth is limited more by soil resources than by light (Forrester, 2014).

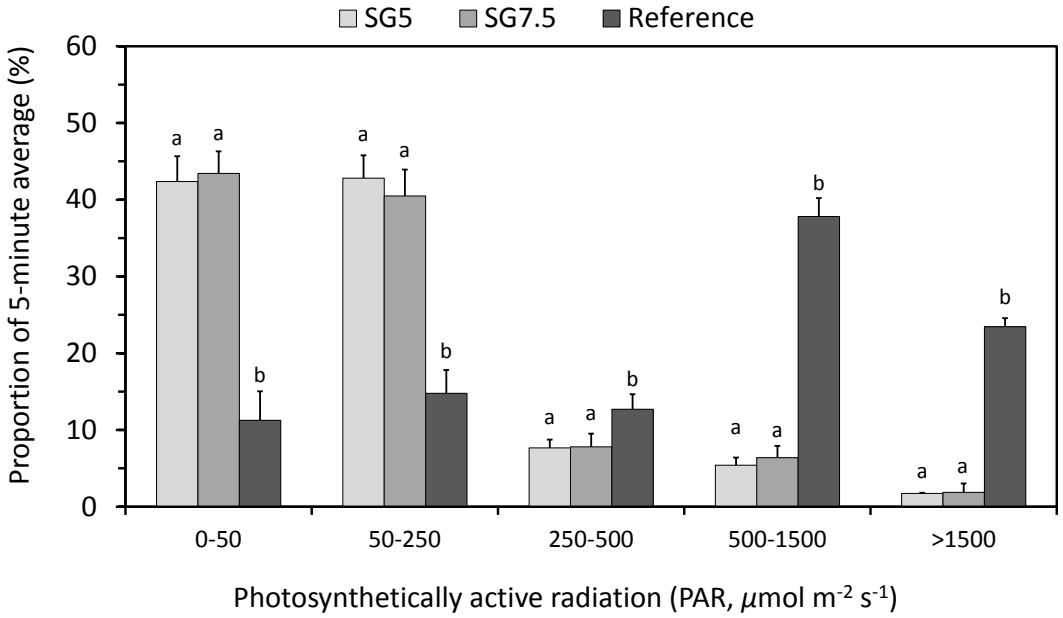

Figure 6.4 Distribution of 5-min averages of photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}) in different intensity classes measured on twelve sunny days under the canopy in 5 m (SG5) and 7.5 m (SG7.5) strip gap in 3.5-yr-old *Acacia* hybrid plantation and open area (reference) in Central Vietnam (mean ± 1 SE; n = 7 for SG0, SG5 and SG7.5, and n = 3 for reference)

6.5. Conclusion

Hopea odorata expressed plasticity in leaf display and branching structure in response to light environment. Biomass growth was positively correlated with APAR. A 2.5- fold difference in relative incident PAR between the gap centre and gap perimeter (60 *v.* 24%) was associated with a higher LUE at the gap centre; however LUE near the gap perimeter may have been partially reduced by water stress at the end of the dry season. In a strip gap where *H. odorata* experienced total light intensities similar to that near the perimeter in the circular gap experiment but a much higher proportion on incident light at levels ≤500 μmol m^{-2} s^{-1}, LUE was much higher, suggesting that the trees were well-

adapted to shade. The *Acacia* hybrid is fast-growing, quickly develops a high leaf area index and expands its canopy to rapidly occupy gaps containing target native species. Therefore, careful timing of interventions is needed to prevent light competition slowing the development of the native species.

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Appendices

Appendix 6.1 Stem diameter ($D_{1.3A}$; $D_{0.3H}$), total height (H_t), live crown length (L_c) and crown diameter (D_c) of sample trees of *Acacia* hybrid and *Hopea odorata* (mean ± 1SD)

Species/ treatment[#]		August 2012				August 2013			
A. hybrid	N	$D_{1.3A}$ (cm)	H_{tA} (cm)	L_{cA} (m)	D_{cA} (m)	$D_{1.3A}$ (cm)	H_{tA} (cm)	L_{cA} (m)	D_{cA} (m)
Circular gap	7	6.5 – 13.8	13.2 – 16.3	2.47 – 7.3	1.7 – 3.0				
Strip gap	7	6.9 – 14.7	10.9 – 15.0	6.8 – 11.1	1.9 – 4.7				
H. odorata	N	$D_{0.3H}$ (cm)	H_{tH} (cm)	L_{cH} (m)	D_{cH} (m)	$D_{0.3H}$ (cm)	H_{tH} (cm)	L_{cH} (m)	D_{cH} (m)
G-1	3	1.00 ± 0.16	1.11 ± 0.12	0.87 ± 0.14	0.71 ± 0.24	1.32 ± 0.33	1.41 ± 0.40	1.15 ± 0.45	0.90 ± 0.37
G3	3	1.17 ± 0.19	1.33 ± 0.22	1.09 ± 0.24	0.77 ± 0.07	1.68 ± 0.38	1.72 ± 0.42	1.51 ± 0.44	0.98 ± 0.09
G6	3	1.58 ± 0.20	1.62 ± 0.19	1.44 ± 0.16	1.02 ± 0.11	2.43 ± 0.43	2.25 ± 0.30	2.02 ± 0.29	1.62 ± 0.36
G9	3	1.80 ± 0.25	2.00 ± 0.14	1.84 ± 0.15	1.50 ± 0.14	2.72 ± 0.40	2.31 ± 0.32	2.10 ± 0.29	1.74 ± 0.41
SG5	3	1.15 ± 0.17	1.35 ± 0.19	1.13 ± 0.17	0.88 ± 0.12	1.65 ± 0.35	1.82 ± 0.38	1.54 ± 0.40	1.32 ± 0.28
SG7.5	3	1.23 ± 0.11	1.47 ± 0.04	1.20 ± 0.08	0.94 ± 0.15	2.00 ± 0.39	1.92 ± 0.41	1.72 ± 0.37	1.75 ± 0.33

[#]Treatments: G-1, G3, G6 and G9 were -1, 3, 6 and 9 m from gap perimeter, respectively; SG5 and SG7.5 were centred along the middle of the 5 and 7.5 m strip gap

Appendix 6.2 Allometric equations for estimation of branch (W_{bA}) and leaf (W_{lA}) dry weight, and leaf area (LA_A) from branch basal area (BA_b) and diameter at breast height ($D_{1.3A}$), and estimation of over- (W_{soA}) and under- (W_{suA}) bark dry stem weight, and over-bark fresh stem weight (W_{sfA}) from $D_{1.3A}$ of 4-yr-old (circular-gap) and 3.5-yr-old (strip-gap) *Acacia* hybrid plantations. Branch diameter was measured at 40 mm from stem

Parameters		Circular gap				Strip gap			
		a	b	n	r^2	a	b	n	r^2
Branch variables ($y = a * BA_{bA}{}^{b}$)									
LZ	W_{bA} (Mg ha^{-1})	44.266	1.560	35	0.98	19.252	1.867	35	0.97
	W_{lA} (Mg ha^{-1})	43.857	1.518	35	0.94	15.219	1.378	35	0.67
	LA_A (cm^2)	5,108.8	1.465	35	0.94	1,808.4	1.540	35	0.79
MZ	W_{bA} (Mg ha^{-1})					54.913	1.358	35	0.97
	W_{lA} (Mg ha^{-1})					44.214	1.232	35	0.91
	LA_A (cm^2)					4,356.5	1.252	35	0.93
UZ	W_{bA} (Mg ha^{-1})	44.484	1.547	35	0.99	47.186	1.352	35	0.96
	W_{lA} (Mg ha^{-1})	72.927	1.223	35	0.99	68.396	1.053	35	0.95
	LA_A (cm^2)	7,158.4	1.227	35	0.99	5,674.4	1.261	35	0.92
Branch variables ($y = 10^{a} * D_{1.3A}{}^{b}$)									
LZ	W_{bA} (Mg ha^{-1})	-2.285	2.158	7	0.74	-0.970	0.987	7	0.12
	W_{lA} (Mg ha^{-1})	-2.459	2.209	7	0.76	-2.048	1.585	7	0.34
	LA_A (cm^2)	-1.419	2.246	7	0.78	-0.853	1.492	7	0.35
MZ	W_{bA} (Mg ha^{-1})					-2.994	3.261	7	0.86
	W_{lA} (Mg ha^{-1})					-3.721	3.711	7	0.94
	LA_A (cm^2)					-2.464	3.521	7	0.95
UZ	W_{bA} (Mg ha^{-1})	-5.964	5.849	7	0.98	-3.244	3.330	7	0.90
	W_{lA} (Mg ha^{-1})	-4.796	4.836	7	0.96	-2.067	2.236	7	0.88
	LA_A (cm^2)	-3.405	4.490	7	0.96	-0.981	2.150	7	0.84
Tree variables ($y = 10^{a} * D_{1.3A}{}^{b}$)									
W_{soA} (kg)		-0.588	2.023	7	0.98	-0.732	2.129	7	0.99
W_{suA} (kg)		-0.690	2.054	7	0.99	-0.847	2.171	7	0.99
W_{sfA} (kg)		-0.209	2.016	7	0.93	-0.287	1.968	7	0.94

[#]LZ: Lower crown zone, MZ: middle crown zone, UZ: Upper crown zone

Appendix 6.3 Allometric equations for estimation of branch (W_{bH}) and leaf (W_{lH}) dry weight, and leaf area (LA_H) from branch basal area (BA_b), and from diameter at 0.3 m above ground ($D_{0.3H}$) and total height (H_{tH}), and for estimation of dry over-bark stem weight (W_{sH}) from $D_{0.3H}$ and H_{tH} of 1- and 2-yr-old *Hopea odorata* planted in a 22-m diameter circular gap within a 3-yr-old and in 5 and 7.5 m strip gaps of a 2.5-yr-old *Acacia* hybrid plantation. Branch diameter was measured at 40 mm from stem

Parameters		1-yr-old					2-yr-old				
Circular gap		a	b	c	n	r^2	a	b	c	n	r^2
Branch variables ($y = a * BA_{bA}{}^b$)											
LZ[#]	W_{bH} (Mg ha^{-1})	0.081	1.308		60	0.93	0.056	1.439		60	0.97
	W_{lH} (Mg ha^{-1})	0.118	1.231		60	0.84	0.234	1.041		60	0.91
	LA_H (cm^2)	13.926	1.261		60	0.84	31.802	0.993		60	0.89
UZ	W_{bH} (Mg ha^{-1})	0.084	1.264		60	0.85	0.066	1.360		60	0.95
	W_{lH} (Mg ha^{-1})	0.238	1.168		60	0.81	0.300	1.041		60	0.87
	LA_H (cm^2)	29.318	1.151		60	0.82	32.986	1.056		60	0.84
Branch variables ($y = a * D_{0.3}{}^b * H_t{}^c$)											
LZ	W_{bH} (Mg ha^{-1})	4.177	3.656	0.209	12	0.98	0.333	6.288	-0.655	12	0.97
	W_{lH} (Mg ha^{-1})	9.103	3.135	0.219	12	0.97	0.685	2.635	2.902	12	0.97
	LA_H (cm^2)	1215.86	2.969	0.258	12	0.97	112.98	2.483	2.701	12	0.97
UZ	W_{bH} (Mg ha^{-1})	1.908	0.955	3.012	12	0.94	4.010	1.733	0.950	12	0.97
	W_{lH} (Mg ha^{-1})	8.841	1.888	0.916	12	0.95	12.491	0.867	1.316	12	0.93
	LA_H (cm^2)	1093.83	1.787	0.936	12	0.94	1301.48	0.322	2.035	12	0.92
Tree variables ($y = a * D_{0.3}{}^b * H_t{}^c$)											
	W_{sH} (kg)	38.649	2.277	0.055	12	0.98	38.649	2.277	0.055	12	0.98
Strip gap		a	b	c	n	r^2	a	b	c	n	r^2
Branch variables ($y = a * BBA^b$)											
LZ	W_{bH} (Mg ha^{-1})	0.043	1.531		6	0.98	0.043	1.531		6	0.98
	W_{lH} (Mg ha^{-1})	0.053	1.595		6	0.91	0.053	1.595		6	0.91
	LA_H (cm^2)	45.318	0.927		6	0.79	9.479	1.478		6	0.88
UZ	W_{bH} (Mg ha^{-1})	0.106	1.179		6	0.71	0.106	1.179		6	0.71
	W_{lH} (Mg ha^{-1})	0.440	0.899		6	0.75	0.440	0.899		6	0.75
	LA_H (cm^2)	40.018	1.005		6	0.81	58.836	0.895		6	0.76
Branch variables ($y = a * D_{0.3H}{}^b * H_{tH}{}^c$ for age 1 yr; $y = a * D_{0.3H}{}^b$ for age 2 yrs)											
LZ	W_{bH} (Mg ha^{-1})	3.634	3.322	0.171	6	0.80	6.044	1.987		6	0.85
	W_{lH} (Mg ha^{-1})	10.427	2.307	0.305	6	0.80	7.079	2.588		6	0.97
	LA_H (cm^2)	1415.21	2.307	0.305	6	0.80	1016.40	2.453		6	0.92
UZ	W_{bH} (Mg ha^{-1})	8.301	4.381	-3.677	6	0.43	1.500	4.546		6	0.99
	W_{lH} (Mg ha^{-1})	19.580	4.607	-3.874	6	0.50	6.280	3.164		6	0.99
	LA_H (cm^2)	2585.09	4.607	-3.874	6	0.50	943.85	2.934		6	0.99
Tree variables ($y = a * D_{0.3H}{}^b$)											
	W_{sH} (kg)	43.978	2.021		6	0.99	43.978	2.021		6	0.99

[#]LZ: Lower crown zone, UZ: Upper crown zone

Appendix 6.4 Parameters of the MAESTRA model for absorbed photosynthetically active radiation (APAR) simulations of *Acacia* hybrid (A) and *Hopea odorata* (H) species. The variable names are as used in the MAESTRA source code and manual (http://www.bio.mq.edu.au/maestra/manual.htm), and the arrays of values are given in the same order. Leaf transmittance, leaf and soil reflectance and crown shape are from le Maire *et al.* (2013)

Species	Parameter name and definition	Value
A and H	lat: latitude	16.3°N
A and H	long: longitude	107.7°E
A and H	notrees: number of surrounding trees	Not specified, all neighbours used
A and H	nolay, pplay, nzen, naz: number of angles and layers to integrate over	6, 12, 5, 11 (default)
A and H	difsky: distribution of diffuse radiation incident from the sky	0 (uniform sky)
A and H	khrsperday: number of timesteps per day	48
A and H	rhosol: soil reflectance in PARa, NIRb and thermal	0.10, 0.3, 0.05
H	atau: leaf transmittance in PAR, NIR and thermal	0.03, 0.32, 0.01
H	arho: leaf reflectance in PAR, NIR and thermal	0.05, 0.25, 0.05
A	atau: leaf transmittance in PAR, NIR and thermal	0.063, 0.296, 0.01
A	arho: leaf reflectance in PAR, NIR and thermal	0.074, 0.206, 0.05
A and H	cshape: crown shape	ELIP (half-ellipsoidal)
A and H	nalpha: number of leaf angle classes from 0^o to 90^o	1
A and H	bpt: beta dist. parameters for the vertical and horizontal leaf area density	uniform

Appendix 6.5 Tree and stand growth variables of the *Acacia* hybrid nurse crop (mean ± 1 SD) during the experiment

Experiment		Circular gap (n = 121)				Strip gap (n = 193)			
Activity		Planting	Planting *H. odorata*	1st yr measurement	2nd yr measurement	Planting	Planting *H. odorata*	1st yr measurement	2nd yr measurement
Tree variables[#]		10/2008	9/2011	8/2012	8/2013	1/2009	9/2011	8/2012	8/2013
$D_{1.3A}$ (cm)			7.7 ± 1.8	9.7 ± 2.0	10.8 ± 2.4		7.5 ± 1.7	10.9 ± 2.1	12.9 ± 2.6
H_{tA} (m)			10.5 ± 1.4	14.7 ± 1.9	17.3 ± 2.2		9.1 ± 1.3	13.5 ± 1.6	17.5 ± 2.3
L_{cA} (m)			3.9 ± 1.1	4.0 ± 1.2	4.2 ± 1.4		6.2 ± 1.2	9.0 ± 1.7	10.1 ± 1.8
D_{cA} (m)			2.0 ± 0.4	2.2 ± 0.6	2.2 ± 0.5		2.5 ± 0.6	3.3 ± 0.8	3.5 ± 0.9
θ_{lA} (°)	LZ			45.0 ± 15.4				41.5 ± 11.2	
	MZ							46.5 ± 13.0	
	UZ			33.4 ± 14.5				39.2 ± 13.9	
θ_{bA} (°)	LZ			63.6 ± 23.4				50.8 ± 10.7	
	MZ							58.9 ± 15.6	
	UZ			52.4 ± 27.2				52.5 ± 21.0	
Stand variables[#]		10/2008	9/2011	8/2012	8/2013	1/2009	9/2011	8/2012	8/2013
Stand density (trees ha^{-1}; m × m)		2,500 (2 × 2)	2,160	2,160	2,160	1,330 (2.5 × 3)	1,088	1,088	1,088
W_{bA} (Mg ha^{-1})				4.06				6.93	
W_{lA} (Mg ha^{-1})				4.22				4.66	
LA (m^2 ha^{-1})				46,555				50,098	
W_{soA} (Mg ha^{-1})				59.4				38.4	
W_{suA} (Mg ha^{-1})				50.5				32.6	
W_{sfA} (Mg ha^{-1})				139.9				72.3	

[#] Stem diameter ($D_{1.3A}$), total height (H_{tA}), crown length (L_{cA}), crown diameter (D_{cA}), leaf angle (θ_{lA}), branch angle (θ_{bA}), branch weight (W_{bA}), leaf weight (W_{lA}), leaf area (LA), dry over- and under-bark stem weight (W_{soA} and W_{suA}), and fresh over-bark stem weight (W_{sfA}); LZ: Lower crown zone, MZ: Middle crown zone, UZ: Upper crown zone

Chapter 7

CONCLUSION AND RECOMMENDATION

This chapter summarises the findings from this study in the context of matching site requirements of *H. odorata* with site conditions when grown with an *Acacia* hybrid nurse crop. The focus is adaptation of *H. odorata* to the key environmental variables experienced in this mixed-species system. The recommendation for application of the findings to rehabilitate degraded landscapes in Vietnam is also discussed.

7.1. Site requirements of *H. odorata* and matching these with site conditions developed under *A*. hybrid plantations

7.1.1. Light requirement and response to nurse acacia plantation

The range of photosynthetically active radiation (PAR) found in this study for the development of *H. odorata* seedlings/saplings was from 11% incident PAR in its natural habitat to 60% incident PAR when grown with an *A.* hybrid nurse crop. This indicated that while *H. odorata* is a shade-tolerant species, even at a young age it is adapted to a relatively wide range of irradiation, and can quickly adapt to a marked increase in radiation. The increasing growth rate and biomass production with increasing available PAR also suggest that at least moderate light levels are required to produce acceptable rates of growth; conversely, heavily shading is likely to compromise growth. Although incident PAR levels > 60% were not tested in this study, a trend of declining of growth rate suggested that an optimum level of radiation may have been reached at this stage

of sapling growth and development. As previous studies have shown that a full-sunlight treatment is associated with low light-use efficiency, poor form (Lee *et al.*, 1997) and lower survival and growth rate (Norisada *et al.*, 2005; McNamara *et al.*, 2006), some level of shading is probably necessary for optimising growth rate and stem quality.

The benefits of higher levels of incident PAR were also associated with higher light interception and light-use efficiency; the greater leaf area of individuals led to the higher light interception and trees which captured more light had higher light-use efficiency. This was also associated with higher photosynthetic rates because of adjustments to leaf architectural and chemical traits. The significantly higher level of light saturation of photosynthesis than associated with shade-adapted leaves showed that seedlings of *H. odorata* were able to develop leaf traits more typical of sun- rather than shade-adapted species when planted in high light environments.

For the *H. odorata* planted in the large gap, the longer the exposed time to full sunlight, the closer leaf traits appeared to become to sun plant leaves e.g. high leaf thickness. This may have been partially affected by ontogenetic effects when trees get older. However, examination of A_{sat}, the biochemical parameters V_{Cmax} or J_{max} and leaf chlorophyll content two years after the *H. odorata* was established indicated no treatment differences, showing that even close to the gap perimeter, there had been sufficient exposure to high irradiation for sun-plant traits to develop.

As light clearly determines the growth rate of *H. odorata,* competition for light in nurse-crop systems needs to be managed. The canopy and height growth of *Acacia* hybrid nurse crops is very fast, and with the planting densities commonly adopted in Vietnam (up to 2,000 trees ha^{-1}), canopy closure will occur in the second year of growth.

This study has shown that the high levels of competition for light will then suppress the growth of the *H. odorata* if there is no immediate intervention.

7.1.2. Soil moisture requirement

The very high densities of natural regeneration found in low lying and wet areas in natural forest indicated that *H. odorata* prefers high moisture levels at this stage in its life cycle. In the very high rainfall wet season in Central Vietnam, there was no indication of water stress. The development of lower leaf water potentials in the *H. odorata* saplings within 3 m of the gap perimeter in the very long dry season indicated that water competition can occur. However, as these measurements were done at the end of the dry season and there was full recovery of moisture levels overnight, *H. odorata* appears to tolerate these levels of stress at this stage in its life cycle. While further investigation is required to find out whether tree growth was significantly affected, care is clearly needed to make sure that more intense levels of water competition are not allowed to develop.

7.1.3. Soil nutrient and other properties

The low soil-nutrient levels observed in its natural habitat indicated that the nutrient requirement for establishment of *H. odorata* seedlings may be small. However, given that the demand for nutrients is positively related with growth rate, in plantations where the supply of light as well as water can be high, the nutrient requirements of *H. odorata* may be much greater. Although the soils at the experimental plantation used in this

study were also low in nutrient concentration, there was no evidence of nutrient deficiency or significant differences in leaf N and P among treatments. Thus the soil nutrient levels were not only sufficient to support high growth rates of the *A.* hybrid, they were also adequate to support the early establishment of *H. odorata* trees. Whether nutrient additions are required by the *H. odorata* as the trees age needs to be investigated.

Acacia hybrid plantations can aid the recovery soil nutrients because of their fast growth and nitrogen-fixing ability; both lead to rapid build-up of soil organic matter and acceleration of the nutrient cycle. In the degraded landscape of Central Vietnam which has had a long history of poor site management, two-to-three 5-yr rotations of *A.* hybrid were adequate to maintain, and in some instances enhance the stock of some key nutrients, though it must be noted that supplementary N, P and K had been added at planting and three-to-six months after planting. There is also an unquantified nutrient removal through the harvesting of commercial products. How the nutrient balance changes in mixtures between *A.* hybrid and *H. odorata* remains to be quantified; the possibility remains that competition for nutrients may not be a constraint on the growth of the native species.

That said, *A.* hybrid plantations were associated with high levels of soil acidity, and there was evidence that pH may decline with time to a high soil acidity level. Interestingly, as there was no apparent effect of soil pH in the range from slightly acidic in natural forest to strongly acidic in *A.* hybrid plantation on growth of *H. odorata*, the species can probably adapt to a wide range of soil acidity. Most degraded upland soils in Vietnam are strongly acidic (Sam *et al.*, 2006; Que *et al.*, 2010), so this characteristic

should enable *H. odorata* to become a potential species for reforestation across a broad landscape.

7.2. Recommendation for application of research results in degraded landscapes in Vietnam

Large areas of degraded lands in Vietnam, a result of war and several decades of unsustainable land-use practices, are associated with the loss of soil nutrient capital, capacity for recycling nutrients, soil acidity and soil compaction; such landscapes resemble the effects of a natural disaster and agricultural production has been completely compromised (Sam *et al.*, 2006). Recovery of these areas to once again become productive lands was recognised by the Vietnamese Government shortly after the 1992 Rio Earth Summit, and some reforestation programs were initiated with the common name "greening the barren lands and denuded hills" (327 Program) and "5 million hectare reforestation program" (5MHRP) (Binh *et al.*, 2004; Jong *et al.*, 2006). The former used mainly monocultures of fast-growing eucalypts, acacias, pine and some "adapted" native tree species (Jong *et al.*, 2006); low financial investment and limited planting techniques however led to little success (Jong *et al.*, 2006). The 5MHRP targeted the recovery of native ecosystems by assisting natural regeneration, enrichment planting and re-establishment of native tree species using nurse-crop planting techniques. The last was the least successful because of inappropriate silviculture practices (Tam, 2007); the key issues were lack of information about site requirements and interactions between planted species.

Vietnam currently has ~14M ha of forests including 10.5M ha of natural forests and 3.5M ha of plantations (MARD, 2013). These are classified into three categories: special-use (nature conservation, protection of historical and cultural relics, tourism, and scientific research), protection (watershed and soil protection), and production (supply of timber and non-timber forest products) (The National Asembly of Vietnam, 2004). For natural forest, about 2M ha of the special-use forests are in good condition with high species richness and standing volume. The remainder, 4M ha of protection and 4.5M ha of production forests are mainly secondary and rehabilitation forests with a history of unsustainable harvesting (MARD, 2011, 2013). These types of forest have low species richness, are especially poor in valuable timber species, have lost capacity for regeneration and recovery owing to lack of seed sources. Instead, the space is occupied by early successional species and bamboos, so there is no receptive seedbed. For plantations, about 2.5M ha are short-rotation monocultures of acacias, eucalypts and pines for low-value products, particularly pulpwood. The rest are mainly protection and special-use plantations, including mixtures of acacias and mixed native-tree species (Tam, 2007; MARD, 2011, 2013). Unfortunately, many commercial plantations use poor silviculture practices, burning slash and litter for land preparation, and clear-cutting of large areas, including those with high slopes; chemical fertilisers are used to boost the nutrient supply. These unsustainable practices trigger huge losses of topsoil due to erosion driven by a highly monsoonal rainfall pattern.

The issues listed above can be categorised as (1) poor regeneration of highly valuable timber species in natural forests, (2) unsuccessful re-establishment and management of the native-tree species plantations, and (3) soil degradation through poor management practices in commercial plantations. The findings from this study

provide ways of addressing these issues for *H. odorata* and *A.* hybrid, and may be applicable to other target species.

7.2.1. Assistance of regeneration of high value species in secondary forests

Secondary forest can be understood as forest regenerating after natural or man-made disturbances (Lamb, 2011b). In principle, the natural succession is the initial appearance of the pioneer species, and then intervening stages before the recovery of the original late successional species. The time for recovery is dependent on the level of degradation (Lamb, 2011b). Thus, following disturbance, light demanding species emerge quickly to occupy the gap; the resulting deep shade compromises the development of understorey seedlings. This is in accordance with the finding in this study that light was a crucial factor controlling the establishment of understorey seedlings of late successional species, though the studied natural forest stand was largely undisturbed. Thus in secondary forest, provision of more light to encourage the development of the understorey seedlings of preferred late successional species is recommended. This can be done by clearance of undesirable vegetation such as shrubs, bamboos, and low-value canopy trees around the target seedlings and saplings. However, it is recognised that light requirements for regeneration and establishment may differ between species, and dictate the level of clearing required.

7.2.2. Re-establishment and management of native tree species plantation on degraded lands

Degraded lands are associated with many difficulties for reforestation. The change of environmental conditions, soil chemical and physical properties, hydrological regimes

and microclimate variables means that the sites no longer provide a habitat for the original tree species (Lamb *et al.*, 2012). The role of *A.* hybrid used in this study was to act as the pioneer species and if possible, quickly recover some ecological benefits to these degraded lands. This study showed that many key soil chemical and physical properties recovered to some degree, and in a way that may support replanting of the native tree species. The exception was soil acidity which may dictate treatment by liming. Thus, using acacia species as nurse crops for re-establishment of native tree species should shorten the recovery process.

For the native *H. odorata*, this study has found that it had a wide range of adaptability to differing levels of light, soil nutrients and soil acidity; it was also able to survive a 6-month dry season in a plantation. However, to optimise growth rate, it is important to know how these native species respond to these variables during different stages of development. Light was the most important for early establishment and development of seedlings, endorsing the practice of enrichment and nurse-crop planting methods as suitable for the re-establishment of these kinds of native-tree species. However, once the seedlings have adapted to the planting environment, more light availability is required to optimise seedling growth. In enrichment planting, the removal of undesirable vegetation to provide adequate light for the target species is necessary. In nurse-crop plantings, manipulation of the shading by timely thinning of nurse crops will reduce light competition. Below-ground resource competition is also a potential constraint on the development of target species. In nurse-crop systems this is linked to the rapid growth rate of the acacia leading to a high consumption of soil nutrients and water. For soil nutrients, the fixation of nitrogen and quick production of litter enable acacias to develop topsoil fertility through nutrient recycling which may be adequate to support the growth rate of the native species. Competition for water in the dry season

remains an unknown quantity; harvesting the acacias to reduce competition for light should also help to diminish this effect. However retention a number of acacia nurse trees is important for supporting the development of acceptable stem form.

7.2.3. Site management for short-rotation commercial plantations

This study has found that *Acacia* hybrid is a potential species for soil recovery in degraded landscapes. In spite of silvicultural practices that were less than optimal, by the second- or third- rotation in Central Vietnam, some key nutrients and soil properties had changed positively. *Acacia* hybrid was also found to be well-adapted to these soils, high productivity being expressed in spite of the acidic soils with low levels of soil nutrients.

The tendency of soil carbon and some soil nutrients to initially decline following planting points to some disadvantages of current management practices. The high levels of element stocks in the first year of the rotation were inherited from the previous rotation. However, the apparent decrease of these stocks in the second year showed that the topsoils were potentially highly vulnerable to erosion and/or leaching in this very high rainfall environment. In the current study these losses were probably exacerbated because the litter layer had been burned. This is a common practice in Vietnam for reducing labour costs, and in the belief that it enhances soil fertility. Burning the organic matter results in instantaneous decomposition of most elements where nutrients are released in available forms for plant uptake; however they can also be easily washed or leached (DeBano *et al.*, 2005). Some such as Na, K, Ca, Mg and P are also lost into atmosphere as particulate matter when the combusting temperature reaches a threshold.

Total nitrogen and total carbon are easily lost by volatilisation in form of gases (DeBano *et al.*, 2005). Burning may also cause the loss of soil macro- and microorganisms which are important for decomposition of organic matter (DeBano *et al.*, 2005). Stopping burning not only conserves soil nutrients but also prevents changes in other soil properties which may be affected due to the loss of organic matter. Whether retention of the organic matter in this study would have affected the result remains unknown.

Clear cutting affects topsoil loss by erosion. The majority areas of forested lands in Vietnam are uplands which range from moderate to high degree of slope. With large areas of non-vegetation coverage and high slope angles, the effect of erosion can be greatly accelerated. Application of strip or patch cutting on slope areas may reduce the impact of run-off water and decrease loss of topsoils. Similarly establishment of monoculture or mixed-species plantations so that a mosaic of different stages of development is captured in the landscape, will also help to reduce erosion.

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14-yr-old *Hopea odorata* plantation Son Tinh, Quang Ngai province.

Photo: Tran Lam Dong, in July, 2008